The Dynamics and Role of Representational Drift

Behavioural and Cognitive Neurosciences Essay

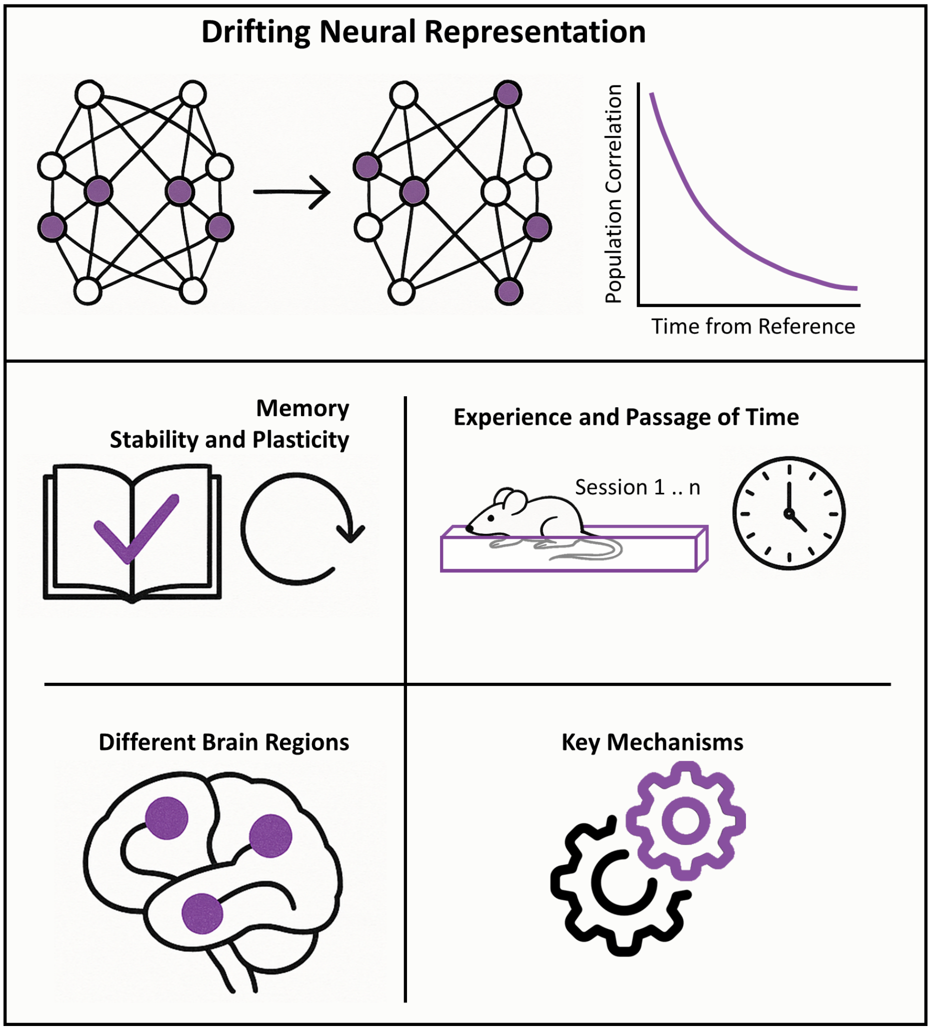
Daniel Grech
S5529093

Supervisor: Prof. Dr. Robbert Havekes

University of Groningen
July 17, 2025

Abstract

The discovery of the memory engram; the trace of a memory encoded by specific patterns of activity across a network of neurons, sparked intense investigation into how memories are stored, maintained, and modified within the brain over time. More recently, it was found that these representations are not static but tend to drift gradually, even as behavior remains stable. In this essay, I aim to understand the role of representational drift by reviewing experimental findings from multiple aspects of this phenomenon. I first discuss how memory representations can remain stable in spite of drift as well as its advantage in allowing for flexible representations. I examine how active experience, as opposed to the mere passage of time, differentially influences the progression of drift. I then review experiments observing drift across different brain regions and their respective dynamics. Possible cellular and network-level mechanisms driving representational drift are also considered. Finally, I attempt to integrate these insights with existing theories of memory and propose future directions for research in this field. Together, this work highlights the importance of drift within neural systems and its contribution within learning and memory.



Contents

1 Introduction

Memory is an integral part of human cognition, enabling us to retain information from our environment, which is essential for learning and adaptation. However, despite its importance, the biological basis of memory has long been a mystery. One of the key concepts in the study of memory is the idea of the "engram", a term coined by the zoologist and evolutionary biologist Richard Semon [2]. Semon proposed that experiences activate neural networks which cause persistent structural changes. These engrams could then be reactivated upon recall by internal or external cues, serving as the biological substrate of memory [2, 3]. Although this hypothesis was initially dismissed, the concept found renewed interest in Donald Hebb's work. Hebb proposed the idea that "neurons that fire together, wire together"; later known as Hebbian plasticity. This theory describes how synaptic connections between neurons are strengthened when they are activated simultaneously [4], and was later supported by experimental evidence with the discovery of long-term potentiation (LTP); the lasting strengthening of synaptic connections between neurons [5]. This led to the idea of engrams as neural representations formed by strengthened synaptic connections which encode memories [5].

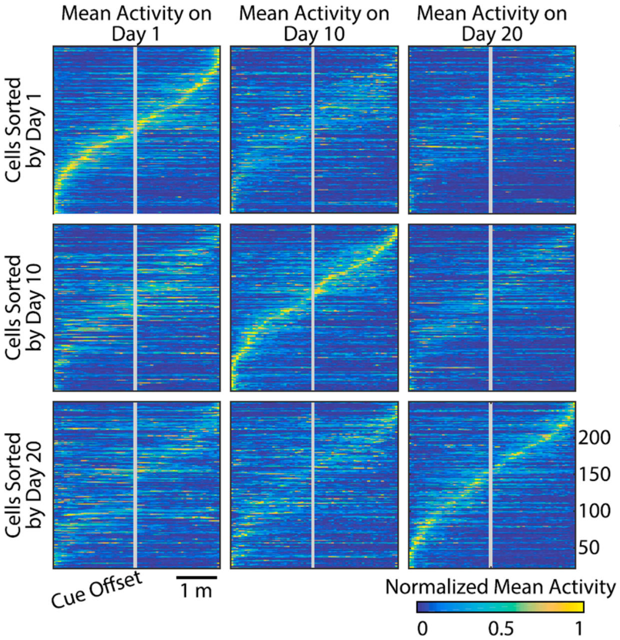


Figure 1: Results presented by Driscoll et al. showing how spatial coding in the posterior parietal cortex drifts over time [1]. Each row represents the calcium signal (averaged over trials) from a single neuron and the horizontal axis corresponds to a task location. When the data is sorted by which neurons were active each day, it is revealed that a different neuronal population codes for location. Over days, the way individual neurons responded to different task locations slowly changed, where some neurons stopped responding to certain places, while others started or shifted where they responded. Reproduced from [1].

In his pioneering experiment, Edward Tolman trained rats to find food in a maze. Later, when confronted with a blocked path, many rats chose a new, shorter route toward the goal rather than relying on the previously learned path [6]. This showed that rats adjust their behaviour according to where they expect goals to be located and provided evidence that spatial memory involves more than simple stimulus-response associations. Instead, Tolman's findings demonstrated that rats can form mental representations of their environment, known as *cognitive maps* [7]. Later neurophysiological experiments highlighted the role of the hippocampus in maintaining cognitive maps, particularly with the discovery of place cells - hippocampal pyramidal cells which exhibit distinct firing patterns when an animal moves through specific locations in its environment [8, 9]. These cells can undergo remapping in response to environmental changes, where a cell can shift its firing rate or location [10]. This phenomenon has been observed for various stimuli, beyond spatial cues [11–19]. In light of this, the concept of cognitive maps has been generalised to apply to episodic memories where facts and events gained from experience are integrated within a contextual framework or network, allowing flexible recall and adaptation to changing circumstances.

It was initially believed that although place cells vary their firing patterns depending on environmental changes, the hippocampal representations which form the basis of the cognitive map remain unchanging over time [20]. However, various studies have revealed that cognitive maps in mice can change drastically in response to the same stimuli, which is generally observed over a period of weeks [1, 13, 15, 21–23]. This phenomenon is known as *representational drift* [24]. Over a timescale of days, only a small number of neurons change their activity, leaving a stable correlation between neural activity and behavioural and environmental factors. However, this change in activity accumulates over a period of weeks leading to a drift over a larger population of neurons. Overall, previously active cells tied to specific variables often lose this correlation, while new neurons adopt these activity patterns, with a few cells even shifting to respond to different variables [25] (Figure 1). Representational drift has been observed in various regions of the brain including multiple subfields of the hippocampus [13, 15, 26–28] as well as cortical areas such as the visual [29], olfactory [23] and motor [30, 31] cortices. It is important to note that although representational drift implies that the brain's internal map of the external world changes over time, others have noted that neural activity often serves more complex computational roles beyond merely representing external stimuli [25]. While it can be useful to generalize neural activity as forming representations in some cases, doing so may limit the range of possible explanations. Instead, as Driscoll and colleagues suggest, it may be more accurate to view neural activity as part of a continuously evolving dynamic system that interacts with the environment, rather than simply creating static representations of stimuli [25].

To investigate representational drift, researchers have employed a variety of experimental approaches. Recent techniques facilitate the recording of large populations of neurons, enabling finer tracking of neuronal activity over time [32–34]. In particular, calcium imaging such as chronic 2-photon imaging [35, 36], allows researchers to observe individual neuronal activity over extended periods of times, possibly up to months [37, 38] and can capture detailed images deep within the brain while causing minimal damage to the tissue [39]. This technique detects light emitted by fluorescent molecules that bind to calcium, allowing researchers to track increases in intracellular calcium levels associated with action potentials. On the other hand, electrophysiology provides a direct measurement of electrical activity through electrodes placed directly in the brain and is often used to monitor place cells and track changes in firing patterns. This enables higher temporal resolution and higher precision in detecting individual spikes than calcium imaging [40, 41]. However, due to its invasive nature, it can cause greater neural tissue damage, especially in long-term studies [42–44]. While the vast majority of the research in this area deals with animal models, some recent studies have explored representational drift in humans [29, 45].

In this essay, I will explore several key aspects of representational drift. First, I will investigate memory and how representational drift may play a part in keeping representations flexible such that they can be updated while maintaining the required stability in memory. I will then analyse how repeated experiences and the passage of time uniquely affect this drift. I will also review how representational drift manifests differently across various brain regions. Next, I will consider the important mechanisms that drive this dynamic process. Finally, in the discussion, I will integrate these insights and assess the purpose of representational drift, as well as exploring future directions for research.

2 Memory Stability and Updating Stored Information

Effective learning requires a balance between stability and plasticity within long-term memory. Representations must be stable enough to be preserved over time, while allowing flexibility in their encoding to enable the integration of new information. To achieve this balance, it is necessary to reconcile these contrasting dynamics, known as the "stability-plasticity dilemma" [46].

2.1 The Stability-Plasticity Dilemma

Excessive rigidity leads to inflexible representations, which impedes memory updating. The entrenchment effect describes the process by which early-learned knowledge becomes deeply ingrained, stabilizing memory representations but limiting flexibility and the ability to acquire new information. On the other hand, excessive plasticity allows new inputs to disrupt existing representations, causing the loss of previously learned information, a phenomenon known as catastrophic forgetting. Representational drift may present a solution to the stability-plasticity dilemma by enabling the coexistence of stable yet adaptable memory representations through dynamic memory ensembles. In fact, research suggests that the hippocampal system supports flexible learning by rapidly encoding new memories and reinstating them in the neocortex for long-term storage [47]. Slow fluctuations in neuronal ensemble activity patterns may act as a "conveyor belt" for memory, providing potential new sites to store memories and updating old ones when the new encoding overlaps [48].

2.2 Maintaining Stability

It is important to understand how behaviour can remain consistent over time despite the occurrence of drift. This can be achieved through redundant representations, which allow for more robust memory. Through "degeneracy", high-dimensional representations encode low-dimensional information, thus allowing multiple configurations to represent the same concept [49]. In fact, there is evidence for this in the context of performing diverse tasks [50–52]. Dimensionality reduction algorithms can be used to analyse population activity in neurons; projecting high-dimensional data to a lower dimension while preserving local structure [53]. In Figure 2a, Rule et al. show how high-dimensional neuronal population activity can contain a low-dimensional task representation (in this case choosing a left or right turn within a maze) [24]. This low-dimensional structure contained within a high-dimensional representation has many degrees of freedom, allowing it to reorganize while maintaining the same topology and local structure. Thus, drift-induced reorganization of the structure still preserves local features needed to decode the structure of the task (Figure 2b). This reorganization can be in the form of changes in tuning [54] or intrinsic excitability [55], which manifests as representational drift. Rule and colleagues also emphasize the concept of 'null-space' which is a subspace in a high-dimensional space that lies orthogonal to some low-dimensional representation [56]. Null-space can explain how the same neuronal population can encode multiple behavioural contexts which is shown in Figure 2c. In a space with a much higher dimension than the encoded information, most random drift occurs within this 'null-space', leaving the primary encoded information unaffected.

2.3 The Role of Representational Drift in Plasticity

While memories must be stable in order to be preserved over time, they must also be updatable in order to adapt to our dynamic environment. Storing representations within flexible activation patterns, which can drift over time, can be advantageous in facilitating learning. In this regard, representational drift may function to provide the "resources" to bind new information [57]. Mau et al., suggest that representational drift, may maximize sampling across the space of possible synaptic connections, making it more likely to find the right synaptic weights necessary to form a new memory or update an old one [48]. Furthermore, changes in synaptic connectivity can modify different neurons' intrinsic excitability, thus changing the likelihood of sub-populations in participating in memory-encoding. In this way, different neuronal sub-populations can be prioritised for encoding or updating of memories across the cortico-hippocampal network [58].

This is demonstrated in the experiment by Driscoll et al., where mice were trained to perform a spatial navigation task within a virtual reality environment [1]. The mice were presented with a visual queue, instructing them to turn left or right to receive a reward and neurons in the posterior parietal cortex (PPC), which are known to be involved in such a task, were monitored. As the mice learned new associations (in the form of novel cues instructing them to turn in a particular direction), neuronal populations that had been previously active for existing representations started exhibiting new activity patterns. This suggests that the same population of neurons can be simultaneously used for learning and memory. Thus, drift may reflect ongoing learning. This is consistent with theoretical work which suggests that plastic neurons are more closely coupled to population activity and may form a flexible layer for learning atop a stable core of low-coupled neurons that maintain a consistent representation [59].

Reflecting on the above, it is clear that the brain is an adaptive system and that drift could play an important role when tackling the stability-plasticity dilemma. Crucially, it is the gradual nature of representational drift that enables learning while maintaining a memory's temporal history and ensuring it remains stable and informative [55]. Appropriate temporal information is vital for the consistency of memory and must be coupled with relevant experiential information. In the next section, I review how representational drift may play a role in the integration of time and experience within memory.

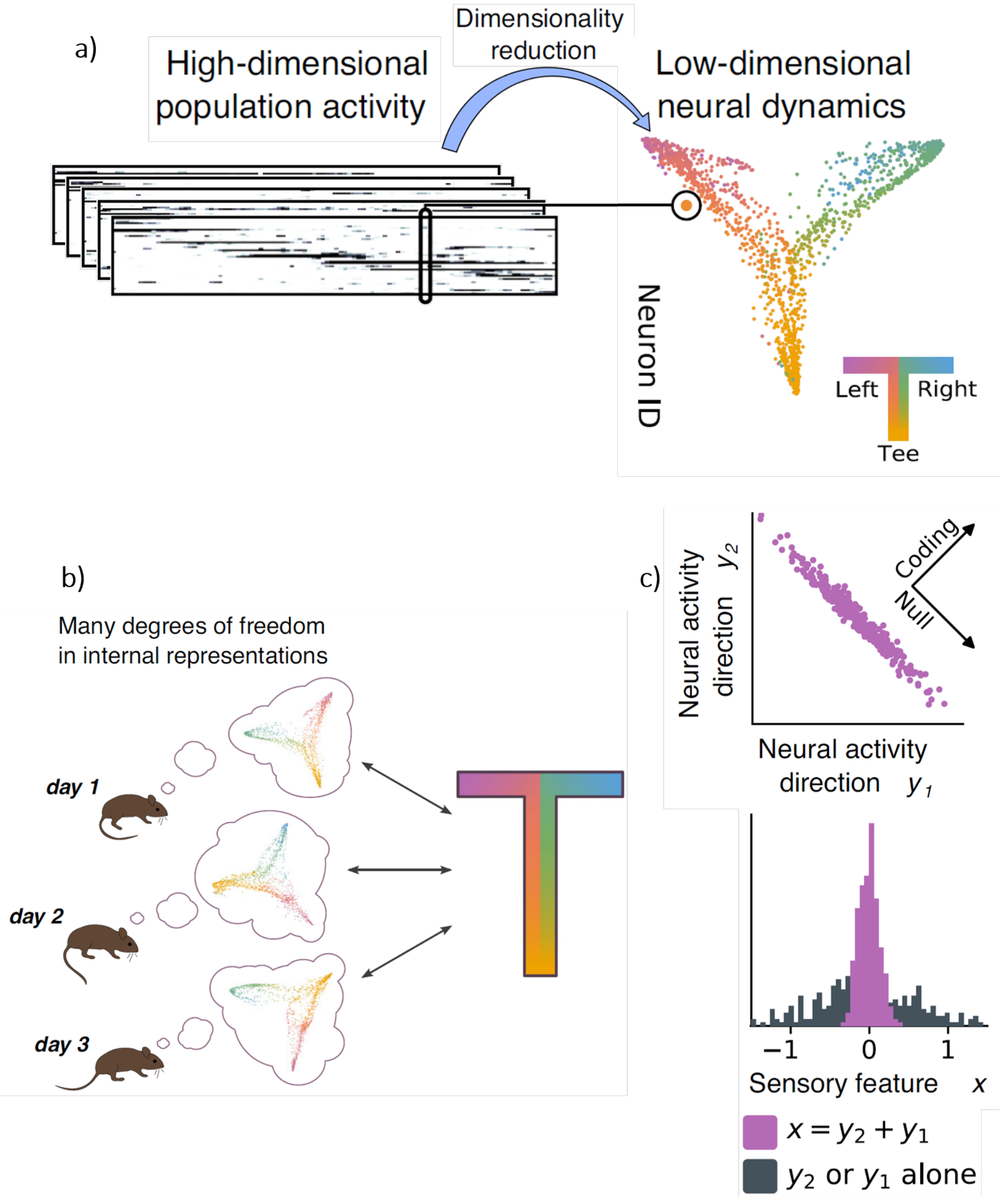


Figure 2: (**a**) Schematic of dimensionality reduction, from a high dimensional space of neuronal population activity, to a lower dimensional task representation; in this case a T-maze. Adapted from [24]. (**b**) How a representation, such as in (*a*) can still preserve local structure such that it can be decoded stably, despite drift. Reproduced from [24]. (**c**) *Top:* Illustration of a sensory variable encoded by 2 components. The spread along the null-space, due to representational drift, occurs orthogonally to the coding of the stimulus. *Bottom:* Such distributed codes can be hard to detect from recordings of only part of the population (like y_1 or y_2 alone), especially if they rely on coordinated activity between different brain areas. Adapted from [24].

3 Experience and the Passage of Time

Representational drift has been suggested to play a part in encoding some temporal component; acting as a form of "timestamping" where memories that occurred close in time are connected while others separated by longer timescales are dissociated [22, 25, 48, 55]. However, other studies have observed drift to be modulated when an animal is repeatedly exposed to the same context [23, 27, 28, 54, 60, 61], implicating active experience in influencing drift. In order to assess the role of representational drift with respect to time and experience, I review the studies by [28] and [61] which examine this relationship in spatial memory.

3.1 Experience-Driven Representational Drift

Khatib et al. sought to dissociate the effect of time and experience on representational drift in mice [28]. They devised a U-shaped maze consisting of two parallel tracks of equal length (labelled A and B), connected by a central box (Figure 3a). Neural activity in the dorsal CA1 region of the hippocampus was recorded as mice explored the tracks. Each session began with 10 minutes of imaging on Track A, followed by 10 minutes of imaging on Track B. However, after recording stopped, mice continued exploring Track B for an additional 180 minutes, accumulating significantly more experience in this environment. The mice then returned to Track A for another 10 minutes of imaging, before a final 10-minute recording session on Track B (Figure 3b). In this setup, the central box acted as a *context switch*, signaling a transition between environments. Analysis revealed that both single-cell correlation, which measures how the activity of individual neurons changes over time, and population vector (PV) correlation, which measures the similarity of activity patterns across a population of neurons between two time points, was found to be significantly lower in the track B recordings compared to track A. Furthermore, positional shift in place fields was significantly higher in track B than track A while rate correlations of the average firing rate of place cells were significantly lower in B. Moreover, the elapsed time between experience seemed to have little effect on representational drift without active experience, as Khatib and colleagues showed in another experiment (Figure 3c,d) [28].

These results indicate that contextual representations drift more when engaged in an experience within that context, such as an animal actively exploring its environment. On the other hand, the mere passage of time has a much weaker effect. Therefore, representational drift may be driven by a context updating mechanism, where memories that are more malleable to change are continually modified [62] and the malleability of these memories is increased as they are used more. A possible reason for this could be that the brain, particularly the hippocampus in these experiments, learns to store (spatial) representations more efficiently with more exposure to a context. This is supported by the fact that the increase in spatial information (SI) content of place cells was significantly higher for track B (where the mouse spent more time in) than track A, whereas the proportion of place cells within the population of active cells was significantly lower (Figure 3e). Furthermore, place cell SI was inversely correlated with the proportion of place cells, suggesting that the encoding capacity remained unchanged, and this was confirmed using a maximum likelihood estimator (MLE) which examined the combined effects of these two factors [28, 63]. Thus, experience within a context may drive representational drift by making memory representations more malleable in order to store information more efficiently, without reducing their accuracy.

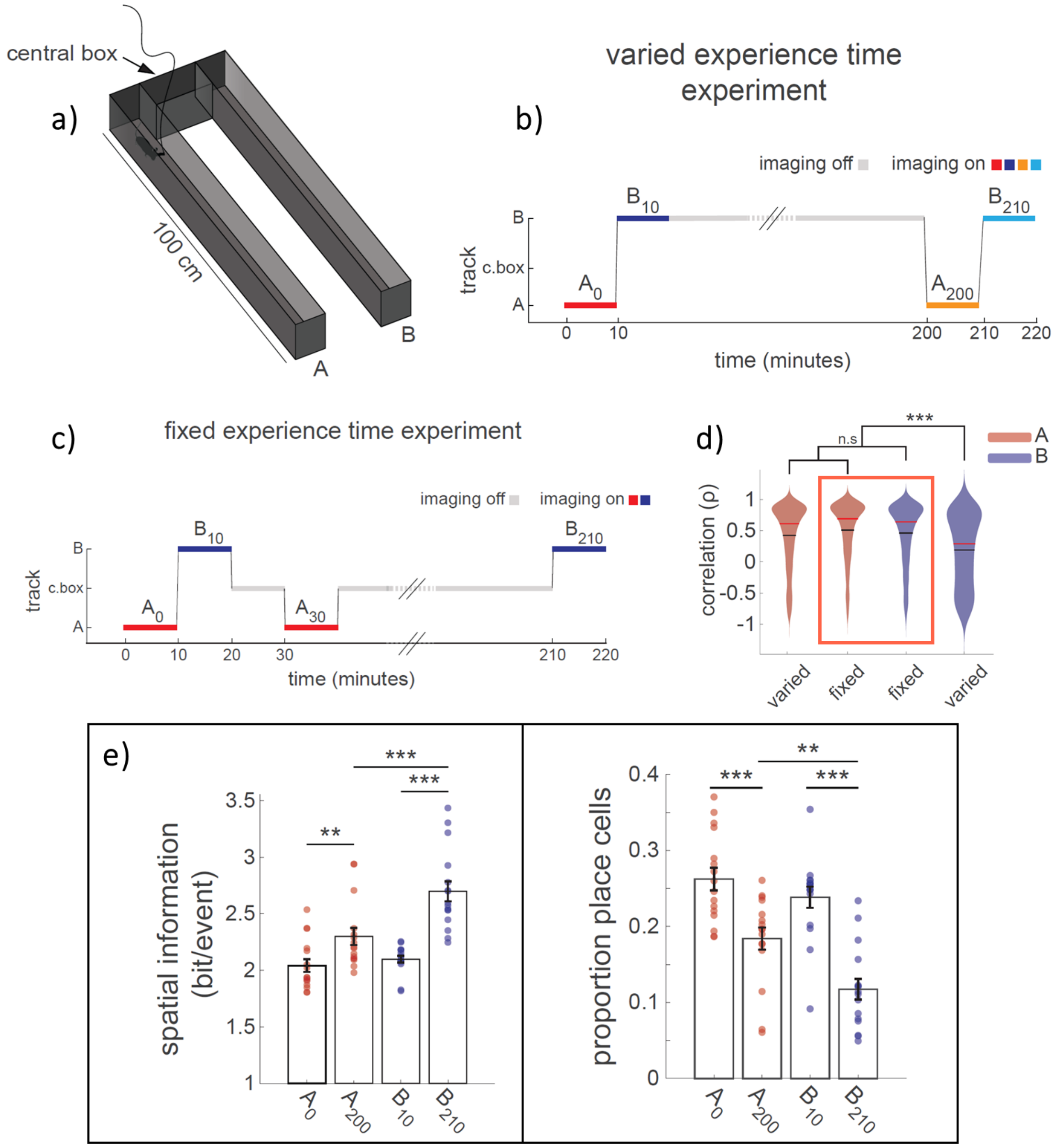


Figure 3: Experience-driven representational drift in Khatib and collegues' experiment [28]. All figures are adapted from [28]. (**a**) Parallel track environment in the experiment consisting of tracks A and B, separated by a central box. (**b**) Timeline of the experiment where mice experienced different amounts of active exploration time across environments. Notably, mice spend much more time in Track B than Track A. (**c**) Timeline of the experiment from where mice experienced the same amount of active exploration time across environments, but experienced different intervals of elapsed time between visits. (**d**) Violin plot showing the distribution of single-cell correlations for the experiments in varied (*b*) and fixed (*c*) experience conditions for tracks A and B. Notably in the fixed experience experiment (results highlighted in the red square), the difference between distributions is not significant (n.s), despite different elapsed time. (**e**) Bar plots for experiment in *(b)*. Subscript next to the letter denotes the elapsed time in minutes. *Left:* Spatial information of place cells for each track. Notably, the increase in spatial information is significantly higher for track B (B_{210}) than track A (A_{200}). *Right:* Proportion of recorded cells classified as place cells for each track. Notably, the decrease in this proportion is significantly more for track B (B_{210}) than track A (A_{200}).

3.2 The Differential Effects of Experience and Time on Representational Drift

While Khatib et al. managed to isolate the effects of time and experience on representational drift, they did not investigate how these components could *differentially* affect drift [28]. Geva et al. explored this by training mice on two different linear track environments (A and B) (Figure 4a) and examining the change in spatial neural code within hippocampal CA1 as mice repeatedly visited the environments [61]. They visited environment A every 2 days and environment B every 4 days. Thus environment A was visited more frequently and had a smaller elapsed time between visits (Figure 4b). This study differed significantly from that of Khatib and colleagues, mainly with respect to two factors; (i) the tracks had dissimilar architectures which resulted in distinct spatial codes and (ii) the experiments took place over a much longer time period, weeks as opposed to hours, with more readings, allowing the tracking of different aspects of drift with respect to time (days) and experiences (sessions). The researchers examined representational drift with respect to neuronal ensemble rate correlation, which quantifies changes in overall activity of neurons across sessions and tuning curve correlation which measures the change in the cells' spatial tuning. In this way, a double dissociation could be revealed between the effects of time and experience by demonstrating how each factor uniquely influences representational drift.

For both environments, the ensemble rate correlation declined at similar rates as a function of time and at different rates when analysed with respect to the number of sessions. This observation suggests that this aspect of drift is driven by the passage of time. On the other hand, the inverse was observed for tuning curve correlations, suggesting that changes in spatial tuning are driven by experience. In particular, the change in spatial tuning was characterised by a shift in existing place fields. These results indicate that different underlying mechanisms contribute to representational drift with respect to different features; changes in subpopulation activity could be caused by alterations in cells' intrinsic and extrinsic excitability [55, 64–67] while spatial tuning could be modulated by changes in synaptic connectivity, mediated by synaptic strength modifications [68] or turnover of dendritic spines [69–71] (refer to Section 5). Additionally, drift in spatial tuning, driven by experience, appears to be context-specific since experience in one environment did not seem to affect drift in the other[1]. This corroborates Khatib and colleagues' results who reported drift proportional to exposure to a particular context and indicates that drift in spatial tuning may reflect optimization of encoding the spatial representation [28]. Moreover, the time-dependent drift in ensemble activity could reflect a context-independent timestamping process, creating a link between experiences, differentiating those that occurred in close succession from those separated by longer time intervals [55, 72, 73].

Time and active experience within a context appear to affect different aspects of representational drift in the hippocampus. Since Khatib and colleagues found no significant effect of time on the decorrelation and position shift in representational activity, the drift mechanisms related to elapsed time seem to have slower dynamics. Indeed, the experiments by Geva et al. which capture the effect of time, took place on a longer time-scale. In line with this, the computational modelling work by Delamare et al. highlights the importance of gradual shifts of intrinsic excitability in order to reconstruct accurate temporal information about past experience [55]. In their model, fluctuations in intrinsic excitability in neuronal ensembles, which manifested as drift, were required in order to distinguish between different time points which is necessary to decode temporal information. However, if the fluctuations were too rapid, neural activity became too random, making it impossible to infer the order of ensemble reactivations. Furthermore, a read-out neuron could only track the drifting ensemble if the fluctuations were slow, reflecting the stability of memory repre-

---

[1] Geva et al. [61] showed this by comparing the similarity in neural patterns between pairs of successive sessions in environment A; first when they were adjacent (A-A) and then when separated by an intermediate session in environment B (A-B-A). There were no differences in spatial tuning metrics between the two pairs, thus concluding that experience in an intermediate environment B did not alter representational drift related to environment A.

sentations in the presence of *moderate* representational drift. On the other hand, Khatib et al. demonstrated that experience-related drift can be observed over shorter time-scales. It makes sense that this drift would be across a dimension related to the particular experience, such as spatial tuning in relation to spatial memory [61], and may reflect a process of encoding representations more compactly, causing finer, more specific changes to representations [28].

Since disentangling time and experience with respect to representational drift has only recently been explored, many questions remain such as how downstream neural circuits adapt to time- and experience-driven drift. Nevertheless, these studies highlight how representational drift is not a homogeneous process, but occurs across multiple dimensions and as such, probably involves different neuronal mechanisms working at the same time. Moreover, while the studies considered in this section have focused on hippocampal activity, representational drift has been observed in other brain regions, exhibiting different characteristics.

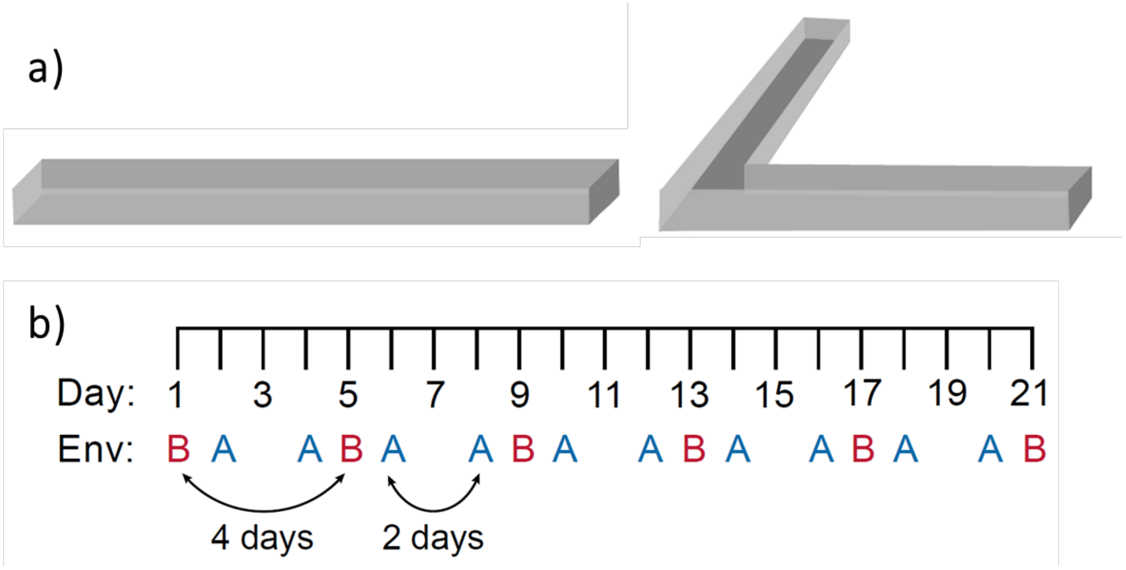


Figure 4: The differential effects of experience and time on representational drift in Geva and colleagues experiments [61]. Both figures are adapted from [61]. (**a**) Different linear track environments used in Geva and colleagues' experiments [61]. (**b**) Experimental timeline where mice visit environment A every 2 days and environment B every 4 days.

4 Representational Drift in Different Brain Regions

In the previous sections, I have focused on representational drift as a phenomenon primarily related to memory, with many studies focusing on drift within the hippocampus [22, 26, 28, 48, 61, 64, 72]. However, similar patterns of drift have also been observed in sensory and motor regions, suggesting that it is a more widespread feature of brain function rather than one limited to memory systems alone. In this section, I review evidence of representational drift across different brain areas, namely the hippocampus, the primary visual cortex, the piriform cortex, and motor-related regions.

4.1 Hippocampus

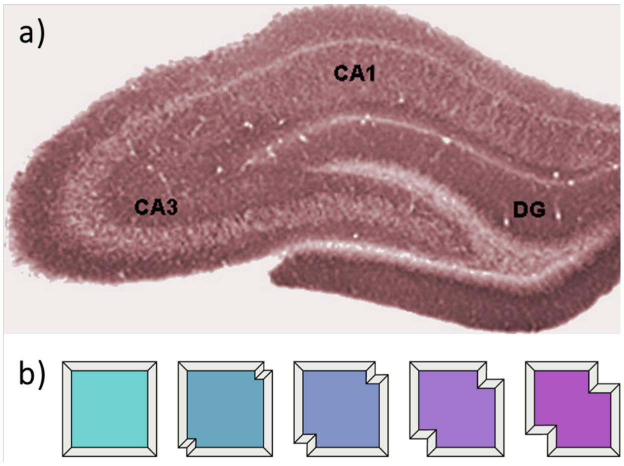


Figure 5: (**a**) Hippocampal subfields of interest in the mouse hippocampus. DG denotes the dentate gyrus. Reproduced from [74]. (**b**) Geometric morphed paradigm, as used in [26]. The far left and right shapes are the two familiar environments, while the shapes in between are intermediate shapes.

Neural recordings from the mouse hippocampus (Figure 5a) have been used extensively to study memory engrams and recordings over a longer-timescale have revealed representational drift and its dynamics in this brain region. The hippocampal subfield CA1, which appears to play a part in maintaining spatial and episodic representations, is the main target of murine brain imaging experiments related to memory, owing to its anatomical accessibility [72]. Furthermore, its prominent place cell activity allows researchers to link behaviour within spatial memory paradigms to the cell recordings. Keinath et at., used a geometric morph paradigm to track how representations in CA1 evolve over time, across gradually changing environments [26]. Unlike other studies which employ only two distinct environments [61], this paradigm includes morphed environments spanning a continuous shape-space between two familiar environments (Figure 5b). The researchers then generated partially correlated hippocampal maps across these changing spatial configurations, which allowed them to monitor how the relative structure of representations evolved over long timescales. In this experiment, long-term changes in the global structure of context representation, characterised by differently shaped environments, where orthogonal to changes related to the passage of time. This meant that cumulative changes related to drift where independent of context identity and indeed, contextual information could be accurately predicted over several weeks, reinforcing the notion of stable memories in spite of drift [48].

Upstream of CA1 lies the hippocampal area CA3 and despite it being less accessible for recording, Sheintuch et al. were able to perform calcium imaging on it [72]. Place cells in CA3 had more stable tuning to spatial cues than place cells in CA1, and this stability seemed to be due to such place cells organizing into assemblies with correlated activity. This is supported by previous studies [27, 75, 76] and reinforces the notion of CA3's auto-associative capabilities due to its large number of recurrent excitatory connections between pyramidal cells [77, 78]. This is in contrast with CA1, where pyramidal cells have more connections with interneurons [79]. These activity dynamics reflect the interaction between different hippocampal subfields and are informative about hippocampal function as a whole. CA3 appears to play a key role in fast, one-shot contextual learning [76, 80, 81] which was also demonstrated by Sheintuch et al., as CA3 place fields carried higher spatial information after the first 3 days of imaging than CA1, demonstrating their ability to quickly respond to novel environments [72]. However, as time passed and the animal became more familiar to the environment, CA1 place cell tuning saw a greater increase, "bridging the gap" between the tuning precision of place fields in these two hippocampal subfields.

Thus, as the downstream target of CA3, CA1 seems to inherit CA3's tuning properties as the animal becomes more familiar with an environment. This "inheritance" of activity is also seen in CA3 from the dentate gyrus, which projects mossy fibres to it [77]. The dentate gyrus appears to carry more stable representations than other hippocampal subfields, experiencing little drift [82], and this stability supports its pattern separation capabilities [83]. CA3 neurons can then receive well separated activity patterns from the dentate gyrus, encoding new memories while reducing interference from older memory traces already embedded in CA3's recurrent connections [84]. Therefore, a hierarchy appears among these hippocampal subfields, where upstream areas, such as the dentate gyrus, are more stable and support pattern separation which act as an anchor for downstream areas, such as CA1, which are more flexible, thus enabling comparison and integration between memories which support generalisation and behavioural adaptability. In this scheme, representational drift emerges as a feature of the flexibility in this system which is also anchored in stable, well-separated codes, striking a balance between stability and plasticity.

4.2 Primary Visual Cortex

Beyond the hippocampus, representational drift has also been observed in sensory brain regions. Early experiments by Hubel & Wiesel, using simple stimuli consisting of lines presented at different angles, revealed that neurons in the primary visual cortex (V1) can be tuned to specific orientations [85]. Orientation tuning appears to form early in development and persist later in life [86]. Indeed, longitudinal chronic 2-photon imaging of mice's V1 across several weeks shows that neural responses remain highly stable for simple artificial stimuli consisting of orientation gratings. However, significant progressive representational drift was observed in response to naturalistic movies [21]. This difference in drift may depend on the connectivity between the subnetworks of neurons, where associations formed earlier in development (such as tuning for orientation) and later reinforced, lead to higher connectivity between neuronal subpopulations [87, 88]. This serves to stabilise tuning properties. On the other hand, neurons which respond to naturalistic stimuli may not belong to such tightly and recurrently connected subnetworks since such stimuli have multiple temporal and spatial features, so two neurons responding to the same frame of the movie do not necessarily respond to the same feature and are not necessarily connected. This leads to greater drift for such stimuli as there is a much smaller stabilising effect.

V1 consists of 6 cortical layers with characteristic cell types and connectivity [89] (Figure 6a,b). One may hypothesise that layers which receive more direct sensory input, such as L4 which receives input from the lateral geniculate nucleus (LGN), would exhibit lower drift than layers which receive more processed input, as they are more constrained by inputs from consistent external stimuli. However, this does not appear to be the case since experimental evidence reveals that a similar amount of drift accumulates across different layers [21, 90] (Figure 7). Moreover, recordings in cortical and subcortical visual areas have revealed the opposite of this hypothesis where areas that are lower in position in the visual processing hierarchy exhibit less stable coding [90]. These compelling results challenge the notion of greater stability with respect to proximity of visual input and implicates a mechanism for stabilising representations as you ascend the hierarchy, possibly through connectivity within recurrent circuits and top-down influence. Representational drift has also been observed for different cell types (both excitatory and inhibitory) in V1 [21, 90]. Also of note is a recent study using longitudinal fMRI data which revealed representational drift in human V1, where neural responsiveness in relation to naturalistic images was likely the source of drift [29]. Finally, Bauer et al. showed that drift in V1 representations are likely driven by the statistics of visual input, possibly through Hebbian plasticity [54]. Taken together, these results indicate that representational drift seems ubiquitous in V1, and may be better quantified as a function of encoded information rather than the histological properties of the cortical layer.

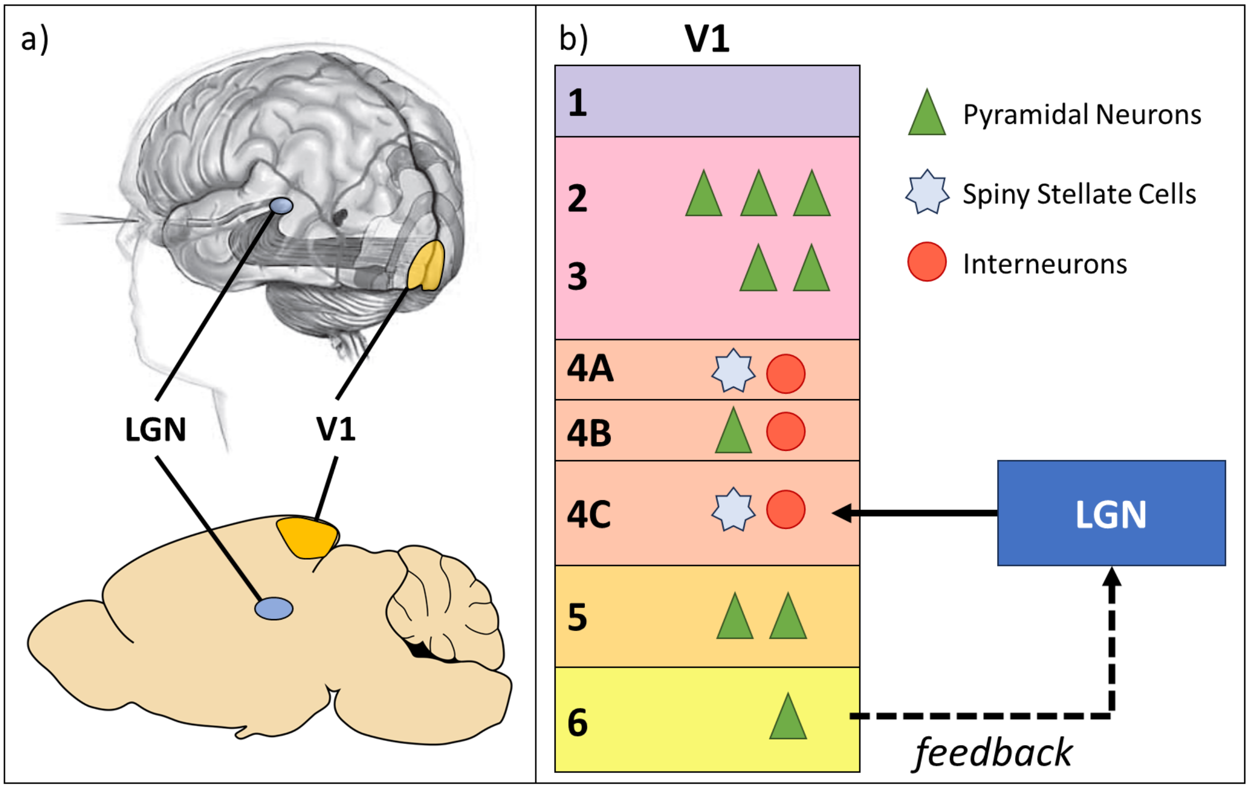


Figure 6: The primary visual cortex (V1) and the lateral geniculate nucleus (LGN). (**a**) Relative location of V1 and LGN within the human *(top)* and mouse *(bottom)* brain. Human brain image is adapted from [91] and mouse brain image is adapted from [92]. (**b**) Schematic of the layers within V1, the types of cells which are mosty present in each layer (note that layer 1 mostly contains transverse fibers with few cell bodies) and basic connections to the LGN. Please refer to [89] for more detail.

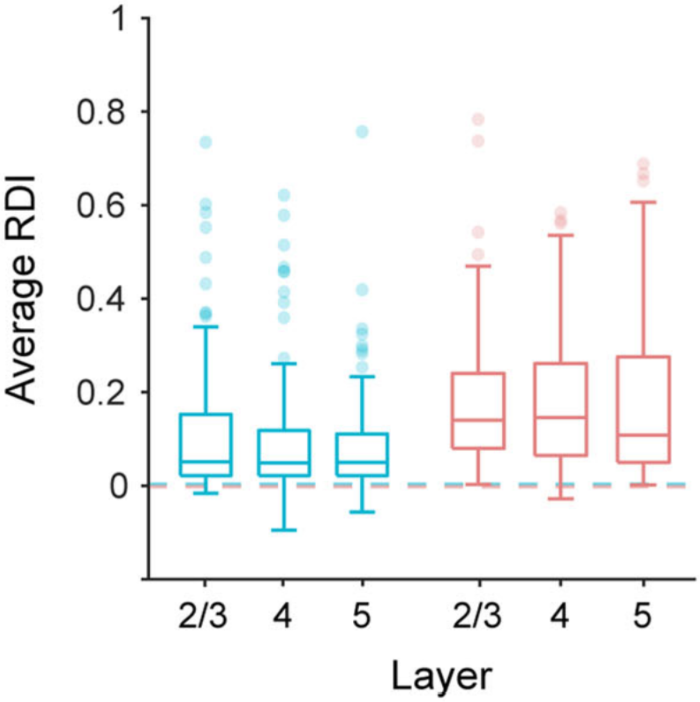


Figure 7: Representational drift quantified across different layers of the primary visual cortex (V1). RDI stands for Representational Drift Index which quantifies the change in single-neuron response stability across sessions, with higher values indicating greater drift between sessions relative to within-session consistency. It is averaged across sessions in this plot. The left 3 boxes (blue) show the session-averaged RDI distributions for the simple artificial stimuli consisting of orientation gratings while the right 3 boxes (red) show this for the naturalistic stimuli, consisting of movies. Reproduced from [21].

4.3 Piriform Cortex

Another sensory area which appears to experience representational drift is the mouse primary olfactory (piriform) cortex as shown by Schoonover et al. [23]. In this study, the researchers demonstrated that the piriform cortex exhibited drift in relation to the same odorant such that the correlation between neuronal activity at different time points approaches 0 within weeks. Furthermore, the geometry defined by population activity in response to a particular odour also changes. This is in contrast to other brain regions such as the hippocampus [22, 48, 93] and visual cortex [21, 29, 54] which exhibit relatively stable population-level structures over time, despite drift in the activity of individual neurons. This indicates that the pirifrom cortex undergoes rapid reorganization over time and another region may contribute to encoding odour identity such that a downstream region could read it out consistently. This is plausible since the olfactory bulb, which exhibits stable responses to odours [94], projects to several different areas apart from the piriform cortex [95]. Fear conditioning did not stabilise the drift, however, repeated exposure to the same odour did temporarily slow down the drift rate. This is in contrast with the results discussed in Section 3, where repeated experience appears to increase drift in hippocampal place cells [28, 61].

4.4 Motor-Related Brain Regions

With regards to movement, representational drift has been observed in brain regions associated with motor learning tasks. In the primate motor cortex and supplementary motor area, tuning with respect to reaching in a particular direction was variable as primates performed the task in familiar and novel environments [30, 96]. Two components contributed to this change in tuning; (i) a learning related component, characterised by systematic shifts in tuning as the animal got accustomed to the novel movements and (ii) a background component, characterised by slow, random drift which was present in both the familiar and novel environments. The slow and random nature of the background changes is necessary to allow for learning [30] and may be indicative of plasticity mechanisms, allowing for more efficient updating of the representation [48]. Furthermore, this drift suggests that the motor cortex is a redundant neural network [30], where motor information is encoded in a high-dimensional space, allowing for drift in multiple directions which are orthogonal to the representation and thus do not affect it [24]. Such redundant coding also seems to play a part in motor representations in the frontal and parietal cortices [1, 31].

In conclusion, representational drift appears to be a widespread phenomenon, present throughout many areas in the brain. These studies reveal the different dynamics of drift in each region, as well as how it is influenced by task-related variables. Taken together, these findings suggest that representational drift is an important feature in neural systems, supporting flexible encoding, storage and learning. In the next section, I review possible underlying mechanisms that may drive this phenomenon.

5 Key Mechanisms

Representational drift is driven by an interplay of neural mechanisms. As discussed previously, drift appears to enhance flexibility in memory representations, supporting the brain's ability to adapt and learn. It is likely that a variety of plasticity-related processes contribute to this phenomenon. In this section, I explore some underlying brain dynamics, including changes that may contribute to directed shifts in activity such as Hebbian plasticity, as well as factors like neurogenesis and synaptic turnover, which may introduce more stochastic variability into neural representations.

5.1 Directed Plasticity Mechanisms in Representational Drift

The role of synaptic plasticity has long been recognized to play a crucial role in learning and memory [4]. In particular, long-term potentiation (LTP) and long-term depression (LTD), two central mechanisms of Hebbian plasticity, are key to shaping these neural adaptations. LTP and LTD respectively enable synaptic strengthening and weakening in response to correlated or uncorrelated neuronal firing [97, 98]. Researchers have used optogenetics to demonstrate a causal link between these processes and memory by directly inducing LTD to deactivate a "fear memory" and LTP to reactivate it [99]. The interaction between LTP and LTD in the hippocampus has also been studied in spatial memory, where LTP has been linked to the formation of associative memories of the environment, while LTD allows the modification of this representation [100]. In the context of representational drift, Bauer et al. showed that when mice were exposed to only a single orientation (by using cylinder lens goggles to limit visual input) the tuning of neurons to a preferred orientation drifted towards the experienced orientation [54]. Their network model revealed that while synaptic volatility (implemented as a random component) caused a random drift in neuronal tuning, Hebbian mechanisms biased the drift towards the input orientation. Therefore, when exposed to many orientations, as in normal vision, Hebbian plasticity may counteract synaptic volatility and stabilize representations. A similar stabilising effect (ie. reduced drift rate) has been observed in the mouse piriform cortex when exposed to the same odour daily [23]. On the other hand, repeated experiences seem to invoke increased drift in the hippocampus (see Section 3 and [28, 61]). Bauer et al. suggest that this difference may be explained by more intense Hebbian plasticity in the hippocampus which may cause connections to shift faster and result in a more exploratory neural pattern [54]. However, this has not been experimentally validated and it may be due to another reason such as the difference in complexity between sensory and spatial memory representations [54, 101].

The interaction between intrinsic synaptic properties and prior plasticity influences neural network dynamics and may explain the gradual shifts in neural representations over time. Migliore et al. used a computational model of a hippocampal CA1 pyramidal neuron to demonstrate how different initial synaptic conditions, such as prior potentiation, and baseline properties like peak conductance, can affect the initiation of LTP and LTD [102]. These findings suggest that differences in synaptic history (such as previous LTP or LTD) and baseline characteristics might contribute to subtle, ongoing modifications in network activity. In this way, representational drift may be driven by gradual changes in neuronal states, which could occur even without new learning experiences, and could lead to a change in neural codes without disrupting the overall stability of the representation.

5.2 Stochastic Drivers of Representational Drift

Another form of plasticity involves changes in intrinsic excitability. Intrinsic excitability is defined as the likelihood for a neuron to generate action potentials when stimulated. Synaptic turnover and remodelling can affect which neurons are more likely to fire, leading to different intrinsic excitability across neuronal ensembles. A neuron's intrinsic excitability can be quantified experimentally by measuring various parameters including afterhyperpolarization and spike frequency accommodation (see [66], Box 1 for details). Fluctuations in intrinsic excitability have been linked to memory allocation since neurons with increased excitability are more likely to participate in an ensemble encoding a particular memory [64–67]. With respect to representational drift, Delamare et al. showed that the emergence of drifting ensemble behavior, which is stable enough to encode memories, is possible through slow fluctuations of neuronal intrinsic excitability [55]. The researchers demonstrated this using a rate-based plastic (specifically following a Hebbian rule to update synaptic weights) recurrent neural network which simulated the initial encoding of a memory followed by subsequent reactivation events. They observed a drift in the network's recurrent weights and could successfully decode the memory using a read-out neuron with plastic weights. Importantly, the output neuron could only track the drifting ensemble (necessary for memory decoding) when the drift was sufficiently gradual. This was only possible if the excitability fluctuations were sufficiently slow, providing a theoretical prediction for the required fluctuation dynamics.

Neurogenesis may induce similar fluctuations since the introduction of new neurons into existing networks would alter the composition of properties of neuronal ensembles. Adult neurogenesis[2] has been shown to play an important role in memory flexibility which makes learning possible [103]. Adult neurogenesis primarily occurs in the dentate gyrus of the hippocampus, specifically in the subgranular zone where neural stem cells divide and produce new neurons [104–106]. Adult neurogenesis may trigger synaptic reorganization, enabling the creation of new activity patterns and the removal of obsolete ones, thereby facilitating memory updating [103, 107]. This feature can be compared to dropout, which is a technique used during training of artificial neural networks where a proportion of nodes are randomly deactivated in order to prevent overfitting [108]. Aitken and colleagues showed that the features of representational drift were geometrically similar to the activity in artificial neural networks when dropout is applied [109]. In this context, representational drift may help to generalise over learned information more effectively. However, in humans, there is ongoing debate about how much adult neurogenesis actually occurs [106, 110–113], and even when it is observed, it seems mostly limited to the hippocampus [114, 115], despite representational drift being observed in other brain regions, as discussed in Section 4. Furthermore, while adult neurogenesis is mostly observed within the dentate gyrus and this region displays very stable representations; experiencing minimal drift (refer to Section 4.1). This makes adult neurogenesis unlikely to be the primary driver of representational drift.

In light of this, continual synaptic remodeling emerges as a more widespread and plausible mechanism which may influence representational drift by creating differing initial synaptic conditions [48, 116, 117]. Indeed, spontaneous synaptic turnover has been observed in cell cultures, even when action potentials are blocked [118, 119] indicating a possible mechanism for drift at the neuronal level. High turnover of dendritic spines has been observed in the hippocampus, where complete turnover has been estimated to occur within weeks [69, 70]. Furthermore, other experiments show that the frequency of dendritic regeneration in CA1 of the hippocampus may influence how accurately place cells represent specific locations in the environment and whether their place fields remain stable or fade over time [71]. This implies that synaptic turnover within dendritic regions might disrupt the processes occurring there, potentially causing place fields to become unstable throughout the entire neural population. Synaptic turnover has also been observed in other

---

[2] The process by which new neurons are generated in specific regions of the adult brain, and integrated into existing neural circuits. Differs from prenatal neurogenesis.

brain regions, including the visual cortex [120], the somatosensory cortex [121] and the frontal cortex [122], possibly contributing to drift in these regions. Representational drift driven by synaptic turnover likely has a more random, background character [30] compared to the more directed shifts in population activity which may be expected to be produced by LTP and LTD. However, it is important to note that a causal link between synaptic turnover and representational drift has not yet been experimentally established, as this would require the technically demanding task of simultaneously imaging dendritic spine and somatic activity concurrently over extended periods [48].

Together, these mechanisms suggest that representational drift arises from a combination of structured, activity-dependent plasticity and ongoing background processes. While LTP and LTD can bias drift toward behaviourally relevant information, spontaneous synaptic remodeling introduces variability that may support continual learning and memory flexibility. Most research on the underlying mechanisms of representational drift remains theoretical or speculative, as establishing a direct link between cellular processes and shifts in neural representations is technically challenging and often limited by current experimental methods. Future work combining long-term imaging and precise manipulation of synaptic and cellular properties will be crucial to directly test these hypotheses and uncover the specific contributions of different mechanisms to representational drift.

6 Discussion

The findings reviewed in this essay highlight that representational drift is not merely a byproduct of noise or instability, but rather an intrinsic and potentially functional feature of neural systems. As discussed by Rule et al., encoding low-dimensional task information as a high-dimensional representation allows for drift in many orthogonal directions while maintaining a stable local structure [24, 53]. Meanwhile, ongoing drift allows for malleable representations, allowing for a substrate which readily binds new memories during learning [48, 64, 66]. Furthermore, it is possible that such drift reflects ongoing reorganization of cognitive maps [7], and can be integrated into several memory consolidation theories. According to Standard Consolidation Theory (SCT), memories initially reliant on the hippocampus are slowly transferred to more stable neocortical networks [123, 124]. In this scheme, representational drift may reflect this dynamic transition, with hippocampal representations remaining flexible while cortical traces stabilize. Conversely, in Indexing Theory, the hippocampus acts as an index linking distributed cortical elements of a memory [125, 126]. Recall that within the hippocampus, upstream areas like the dentate gyrus exhibit stable representations and better pattern separation capabilities while downstream areas like CA1 exhibit more drift (Section 4.1). This hierarchical organization of drift within the hippocampus suggests that stable indexing might be maintained upstream, while downstream flexibility permits dynamic updating of memory features as new information is integrated. Thus, representational drift may bridge aspects of Standard Consolidation Theory and Indexing Theory, enabling the hippocampus to flexibly update memory indices while facilitating the distribution and consolidation into cortical areas.

The experiments by Khatib et al. [28] and Geva et al. [61] reviewed in Section 3 suggest a role for representational drift in handling experience and time within memory. Both studies reported increased cumulative drift as a function of active experience. This is consistent with the idea in Multiple Trace Theory (MTT) that each retrieval or re-encoding of a memory creates a new, slightly altered trace [127, 128]. A particularly interesting result is that spatial information (SI) content in place cells increased while the proportion of place cells within active cells decreased with more exposure to a particular context [28]. This may reflect a compaction of the contextual representation as information is stored more efficiently with repeated exposure. This also fits into MTT which predicts that elements within episodic memories gradually undergo abstraction, eventually being stored as a “gist” representation in the neocortex as part of semantic memory. The decrease in proportion of active place cells may reflect this migration. This could also tie into a model proposed in a recent article by Kolibius et al. which reconciles two frameworks: concept neurons, which encode specific elements of an experience, and index neurons, which link distributed memory features [129]. The authors suggest that, over time, index neurons evolve into concept neurons as a result of accumulating overlapping memory traces. The increased SI [28] may reflect the integration of overlapping memory traces, potentially mediated by shared excitability mechanisms. Thus, within this more unified framework, increased representational drift due to experience may reflect an evolution of indices based on patterns extracted from experiences which eventually lead to neurons tuned to a general concept (for example coarse spatial features within an environment). Eventually, semantic memories can be borne out of overlapping episodic features. A similar concept has been employed in computer systems to create more adaptive database indexes [130].

The presence of representational drift throughout the brain reinforces the idea that it operates as a unified, adaptive system, with representations distributed across widespread neural circuits. In this respect, corrective feedback would be required among brain regions in order to maintain consistent distributed representations in spite of accumulating drift. As observed in some sensory cortices (reviewed in Section 4), external cues may serve to stabilise memory representations [23, 54]. In absence of these cues, internal error signals relayed between interconnected brain regions could help preserve consistency within distributed representations [24]. This scheme ties into the concept of predictive coding and suggests that internal representations between brain regions are compared as well as with incoming sensory input. I note that to my knowledge, the existence of such error signals has never been experimentally probed. This would require longitudinal recordings from multiple brain regions in parallel and it would be challenging to disentangle such error signals from other processes. Nevertheless, integrating such error signals within a theoretical framework and observing network dynamics within a computer model is a compelling possibility and can shed light on how plasticity from one brain region can be guided based on feedback from another.

In Section 5, I reviewed how representational drift is likely the result of plasticity mechanisms which may be directed like LTP and LTD, as well as stochastic, like fluctuations in intrinsic excitability and synaptic turnover. These mechanisms seem especially prevalent in the hippocampus [66, 69, 70, 97, 114, 115], creating a dynamic environment conducive to both memory formation and updating. Thus, the hippocampus appears to play a central role during learning, as evidenced by the synchronization of neocortical activity with hippocampal sharp-wave ripple (SPW-R) events[131, 132]. SPW-Rs are high-amplitude, short-duration waveforms generated by highly coordinated hippocampal neuronal activity, and are closely linked to phenomena such as replay and preplay. During replay, sequences of neurons activated during experience are reactivated in reverse order and at a compressed timescale, typically during offline brain states such as sleep [133]. In contrast, preplay refers to the sequential activation of neurons in the correct order, reflecting potential future trajectories [134, 135]. In spatial memory tasks, replay involves the reactivation of place cells corresponding to previously explored paths in reverse, while preplay activates cells along possible future routes. In this way, representational drift could be a result of these SPW-R dynamics; replay patterns, which occur after a learning experience, may subsequently serve as preplay templates, facilitating the integration of upcoming, related experiences. In this scheme, a representation triggered by a particular context, such as a spatial location, could also encode exploratory motifs which are cyclically refined after replay-preplay episodes. Consequently, drifting neural activity is observed, even in the presence of unchanging stimuli. A recent study by Maboudi et al. showed how SPW-R representations during sleep predict future place fields in a spatial memory task, even when these place fields change between sessions [136]. This further supports the notion of a link between representational drift and replay-preplay episodes during sleep [136].

Despite mounting evidence of representational drift, where neural activity changes while stimuli and behaviour remain the same, ambiguity remains around its manifestation. The studies reviewed here implicitly assume that a particular context reactivates the same memory trace which then gradually decorrelates over time or with repeated experience. However, could this interpretation be misleading? Re-exposure to the same stimuli or task may form a new memory rather than simply reactivating a previous representation. Furthermore, even if the same, context-related engram is being tracked throughout the experiment, more information may be added to the memory as new details or associations are incorporated. This may be due to subtle changes in the experience itself, such as different paths taken during spatial learning tasks, or from internal factors like fluctuations in attention between sessions. While these confounds are very difficult to control for, recording other physiological measures such as pupil size and heart rate may provide valuable proxies for arousal and attentional state and can offer insight into how internal variability can influence representational dynamics. Nevertheless, careful consideration is necessary when interpreting such results and their implications for memory formation and maintenance.

The study of representational drift is relatively recent, largely driven by advances in technologies that allow for long-term, longitudinal recordings of neural activity. As a result, many promising avenues remain open for future exploration. Techniques such as optogenetics could be used to manipulate neural activity with high precision, helping to uncover the mechanisms underlying drift. For instance, researchers could selectively reactivate or inhibit traces of specific spatial memories and observe the resulting effects on neural dynamics [137]. Additionally, further experiments are needed to investigate representational drift in humans, following approaches similar to those used by Roth et al. [29]. Of course, this research faces several limitations compared to animal models since less invasive techniques only provide an indirect measure of neural activity, making it much harder to quantify the drift. Furthermore, since researchers cannot manipulate specific neurons, interpreting the underlying mechanisms of representational drift becomes more complex and requires careful extrapolation. Nevertheless, human studies can incorporate complex cognitive tasks, such as memory recall, decision-making, or problem-solving and explore representational drift with more naturalistic memories which are difficult to simulate in animal models. Finally, new models of memory and learning should make predictions that are consistent with the observed drift dynamics.

7 Conclusion

In this essay, I have reviewed several facets of representational drift in order to understand its role within the brain. I have reviewed its function within memory, serving to keep representations plastic, while preserving population structure to maintain stability. I then examined how representational drift is influenced by active experience and the absolute passage of time, drawing on insights from two recent studies [28, 61]. Next, I explored how drift manifests differently across brain regions and the importance of the type of information being encoded. Finally, I considered the underlying neural mechanisms that contribute to drift, identifying both directed plasticity processes, such as LTP and LTD, and more stochastic processes, including fluctuations in intrinsic excitability and synaptic turnover. Taken together, these findings suggest that representational drift is not merely noise, but a fundamental feature of neural systems, enabling the brain to flexibly encode, update, and integrate information over time while preserving stability, thus making it an important mechanism for effective learning.

References

1. Driscoll, L. N., Pettit, N. L., Minderer, M., Chettih, S. N. & Harvey, C. D. Dynamic Reorganization of Neuronal Activity Patterns in Parietal Cortex. eng. *Cell* **170,** 986–999.e16. ISSN: 1097-4172 (Aug. 2017).
2. Semon, R. W., Lee, V. & Duffy, B. *Mnemic psychology* **2 p. l.,7-344 p.** `https://catalog.hathitrust.org/Record/005764416` (Macmillan, New York, 1923).
3. Schacter, D. L., Eich, J. E. & Tulving, E. Richard Semon's theory of memory. en. *Journal of Verbal Learning and Verbal Behavior* **17,** 721–743. ISSN: 00225371. `https://linkinghub.elsevier.com/retrieve/pii/S0022537178904437` (2024) (Dec. 1978).
4. Hebb, D. O. *The Organization of Behavior* (Wiley&Sons, New York, 1949).
5. Bliss, T. V. P. & Lømo, T. Long-lasting potentiation of synaptic transmission in the dentate area of the anaesthetized rabbit following stimulation of the perforant path. en. *The Journal of Physiology* **232,** 331–356. ISSN: 0022-3751, 1469-7793. `https://physoc.onlinelibrary.wiley.com/doi/10.1113/jphysiol.1973.sp010273` (2024) (July 1973).
6. Tolman, E. C., Ritchie, B. F. & Kalish, D. Studies in spatial learning. I. Orientation and the short-cut. en. *Journal of Experimental Psychology* **36,** 13–24. ISSN: 0022-1015. `https://doi.apa.org/doi/10.1037/h0053944` (2024) (Feb. 1946).
7. Tolman, E. C. Cognitive maps in rats and men. eng. *Psychological Review* **55,** 189–208. ISSN: 0033-295X (July 1948).
8. O'Keefe, J. & Dostrovsky, J. The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. en. *Brain Research* **34,** 171–175. ISSN: 00068993. `https://linkinghub.elsevier.com/retrieve/pii/0006899371903581` (2024) (Nov. 1971).
9. O'Keefe, J. *The hippocampus as a cognitive map* 1978.
10. Muller, R. & Kubie, J. The effects of changes in the environment on the spatial firing of hippocampal complex-spike cells. en. *The Journal of Neuroscience* **7,** 1951–1968. ISSN: 0270-6474, 1529-2401. `https://www.jneurosci.org/lookup/doi/10.1523/JNEUROSCI.07-07-01951.1987` (2024) (July 1987).
11. Wood, E. R., Dudchenko, P. A. & Eichenbaum, H. The global record of memory in hippocampal neuronal activity. en. *Nature* **397.** Publisher: Nature Publishing Group, 613–616. ISSN: 1476-4687. `https://www.nature.com/articles/17605` (2024) (Feb. 1999).
12. Anderson, M. I. & Jeffery, K. J. Heterogeneous Modulation of Place Cell Firing by Changes in Context. en. *The Journal of Neuroscience* **23,** 8827–8835. ISSN: 0270-6474, 1529-2401. `https://www.jneurosci.org/lookup/doi/10.1523/JNEUROSCI.23-26-08827.2003` (2024) (Oct. 2003).
13. Kentros, C. G., Agnihotri, N. T., Streater, S., Hawkins, R. D. & Kandel, E. R. Increased Attention to Spatial Context Increases Both Place Field Stability and Spatial Memory. English. *Neuron* **42.** Publisher: Elsevier, 283–295. ISSN: 0896-6273. `https://www.cell.com/neuron/abstract/S0896-6273(04)00192-8` (2024) (Apr. 2004).
14. Moita, M. A. P., Rosis, S., Zhou, Y., LeDoux, J. E. & Blair, H. T. Putting Fear in Its Place: Remapping of Hippocampal Place Cells during Fear Conditioning. en. *The Journal of Neuroscience* **24,** 7015–7023. ISSN: 0270-6474, 1529-2401. `https://www.jneurosci.org/lookup/doi/10.1523/JNEUROSCI.5492-03.2004` (2024) (Aug. 2004).

15. Muzzio, I. A. *et al.* Attention Enhances the Retrieval and Stability of Visuospatial and Olfactory Representations in the Dorsal Hippocampus. en. *PLOS Biology* **7.** Publisher: Public Library of Science, e1000140. ISSN: 1545-7885. `https://journals.plos.org/plosbiology/article?id=10.1371/journal.pbio.1000140` (2024) (June 2009).
16. Kennedy, P. J. & Shapiro, M. L. Motivational states activate distinct hippocampal representations to guide goal-directed behaviors. en. *Proceedings of the National Academy of Sciences* **106,** 10805–10810. ISSN: 0027-8424, 1091-6490. `https://pnas.org/doi/full/10.1073/pnas.0903259106` (2024) (June 2009).
17. Hallock, H. L. & Griffin, A. L. Dynamic coding of dorsal hippocampal neurons between tasks that differ in structure and memory demand. en. *Hippocampus* **23,** 169–186. ISSN: 1050-9631, 1098-1063. `https://onlinelibrary.wiley.com/doi/10.1002/hipo.22079` (2024) (Feb. 2013).
18. Eichenbaum, H. Time cells in the hippocampus: a new dimension for mapping memories. en. *Nature Reviews Neuroscience* **15,** 732–744. ISSN: 1471-003X, 1471-0048. `https://www.nature.com/articles/nrn3827` (2024) (Nov. 2014).
19. Ormond, J., Serka, S. A. & Johansen, J. P. Enhanced Reactivation of Remapping Place Cells during Aversive Learning. en. *The Journal of Neuroscience* **43,** 2153–2167. ISSN: 0270-6474, 1529-2401. `https://www.jneurosci.org/lookup/doi/10.1523/JNEUROSCI.1450-22.2022` (2024) (Mar. 2023).
20. Thompson, L. & Best, P. Place cells and silent cells in the hippocampus of freely-behaving rats. en. *The Journal of Neuroscience* **9,** 2382–2390. ISSN: 0270-6474, 1529-2401. `https://www.jneurosci.org/lookup/doi/10.1523/JNEUROSCI.09-07-02382.1989` (2024) (July 1989).
21. Marks, T. D. & Goard, M. J. Stimulus-dependent representational drift in primary visual cortex. en. *Nature Communications* **12.** Publisher: Nature Publishing Group, 5169. ISSN: 2041-1723. `https://www.nature.com/articles/s41467-021-25436-3` (2024) (Aug. 2021).
22. Rubin, A., Geva, N., Sheintuch, L. & Ziv, Y. Hippocampal ensemble dynamics timestamp events in long-term memory. en. *eLife* **4,** e12247. ISSN: 2050-084X. `https://elifesciences.org/articles/12247` (2024) (Dec. 2015).
23. Schoonover, C. E., Ohashi, S. N., Axel, R. & Fink, A. J. P. Representational drift in primary olfactory cortex. en. *Nature* **594.** Publisher: Nature Publishing Group, 541–546. ISSN: 1476-4687. `https://www.nature.com/articles/s41586-021-03628-7` (2024) (June 2021).
24. Rule, M. E., O'Leary, T. & Harvey, C. D. Causes and consequences of representational drift. *Current Opinion in Neurobiology. Computational Neuroscience* **58,** 141–147. ISSN: 0959-4388. `https://www.sciencedirect.com/science/article/pii/S0959438819300303` (2024) (Oct. 2019).
25. Driscoll, L. N., Duncker, L. & Harvey, C. D. Representational drift: Emerging theories for continual learning and experimental future directions. en. *Current Opinion in Neurobiology* **76,** 102609. ISSN: 09594388. `https://linkinghub.elsevier.com/retrieve/pii/S0959438822001039` (2024) (Oct. 2022).
26. Keinath, A. T., Mosser, C.-A. & Brandon, M. P. The representation of context in mouse hippocampus is preserved despite neural drift. en. *Nature Communications* **13.** Publisher: Nature Publishing Group, 2415. ISSN: 2041-1723. `https://www.nature.com/articles/s41467-022-30198-7` (2024) (May 2022).
27. Mankin, E. A. *et al.* Neuronal code for extended time in the hippocampus. *Proceedings of the National Academy of Sciences* **109.** Publisher: Proceedings of the National Academy of Sciences, 19462–19467. `https://www.pnas.org/doi/full/10.1073/pnas.1214107109` (2024) (Nov. 2012).

28. Khatib, D. *et al.* Active experience, not time, determines within-day representational drift in dorsal CA1. en. *Neuron* **111,** 2348–2356.e4. ISSN: 08966273. `https://linkinghub.elsevier.com/retrieve/pii/S0896627323003872` (2024) (Aug. 2023).

29. Roth, Z. N. & Merriam, E. P. Representations in human primary visual cortex drift over time. en. *Nature Communications* **14.** Publisher: Nature Publishing Group, 4422. ISSN: 2041-1723. `https://www.nature.com/articles/s41467-023-40144-w` (2024) (July 2023).

30. Rokni, U., Richardson, A. G., Bizzi, E. & Seung, H. S. Motor Learning with Unstable Neural Representations. en. *Neuron* **54,** 653–666. ISSN: 08966273. `https://linkinghub.elsevier.com/retrieve/pii/S0896627307003339` (2025) (May 2007).

31. Carmena, J. M., Lebedev, M. A., Henriquez, C. S. & Nicolelis, M. A. L. Stable Ensemble Performance with Single-Neuron Variability during Reaching Movements in Primates. en. *Journal of Neuroscience* **25.** Publisher: Society for Neuroscience Section: BRIEF COMMUNICATIONS, 10712–10716. ISSN: 0270-6474, 1529-2401. `https://www.jneurosci.org/content/25/46/10712` (2025) (Nov. 2005).

32. Jun, J. J. *et al.* Fully integrated silicon probes for high-density recording of neural activity. en. *Nature* **551.** Publisher: Nature Publishing Group, 232–236. ISSN: 1476-4687. `https://www.nature.com/articles/nature24636` (2024) (Nov. 2017).

33. Sofroniew, N. J., Flickinger, D., King, J. & Svoboda, K. A large field of view two-photon mesoscope with subcellular resolution for in vivo imaging. en. *eLife* **5,** e14472. ISSN: 2050-084X. `https://elifesciences.org/articles/14472` (2024) (June 2016).

34. Steinmetz, N. A. *et al.* Neuropixels 2.0: A miniaturized high-density probe for stable, long-term brain recordings. en. *Science* **372,** eabf4588. ISSN: 0036-8075, 1095-9203. `https://www.science.org/doi/10.1126/science.abf4588` (2024) (Apr. 2021).

35. Grienberger, C. & Konnerth, A. Imaging calcium in neurons. eng. *Neuron* **73,** 862–885. ISSN: 1097-4199 (Mar. 2012).

36. Margolis, D. J., Lütcke, H., Helmchen, F., Weber, B. & Haiss, F. en. in *Optical Imaging of Neocortical Dynamics* (eds Weber, B. & Helmchen, F.) 151–173 (Humana Press, Totowa, NJ, 2014). ISBN: 978-1-62703-785-3. `https://doi.org/10.1007/978-1-62703-785-3_10` (2024).

37. Katlowitz, K., Picardo, M. & Long, M. Stable Sequential Activity Underlying the Maintenance of a Precisely Executed Skilled Behavior. *Neuron* **98,** 1133–1140.e3 (2018).

38. Kozai, T. D. Y., Eles, J. R., Vazquez, A. L. & Cui, X. T. Two-photon imaging of chronically implanted neural electrodes: Sealing methods and new insights. eng. *Journal of Neuroscience Methods* **258,** 46–55. ISSN: 1872-678X (Jan. 2016).

39. Rubart, M. Two-photon microscopy of cells and tissue. eng. *Circulation Research* **95,** 1154–1166. ISSN: 1524-4571 (Dec. 2004).

40. Kuzum, D. *et al.* Transparent and flexible low noise graphene electrodes for simultaneous electrophysiology and neuroimaging. en. *Nature Communications* **5,** 5259. ISSN: 2041-1723. `https://www.nature.com/articles/ncomms6259` (2024) (Oct. 2014).

41. Siegle, J. H. *et al.* Reconciling functional differences in populations of neurons recorded with two-photon imaging and electrophysiology. eng. *eLife* **10,** e69068. ISSN: 2050-084X (July 2021).

42. Welle, C. G. *et al.* Longitudinal neural and vascular structural dynamics produced by chronic microelectrode implantation. *Biomaterials* **238,** 119831. ISSN: 0142-9612. `https://www.sciencedirect.com/science/article/pii/S0142961220300776` (2024) (Apr. 2020).

43. Hammer, D. X. *et al.* Longitudinal vascular dynamics following cranial window and electrode implantation measured with speckle variance optical coherence angiography. EN. *Biomedical Optics Express* **5.** Publisher: Optica Publishing Group, 2823–2836. ISSN: 2156-7085. `https://opg.optica.org/boe/abstract.cfm?uri=boe-5-8-2823` (2024) (Aug. 2014).
44. Yang, Y. *et al.* Improved calcium sensor GCaMP-X overcomes the calcium channel perturbations induced by the calmodulin in GCaMP. *Nature Communications* **9** (2018).
45. Kulkarni, N. & Lega, B. C. *Episodic boundaries affect neural features of representational drift in humans* June 2024. `https://elifesciences.org/reviewed-preprints/90576v2` (2024).
46. Grossberg, S. How does a brain build a cognitive code? *Psychological Review* **87.** Place: US Publisher: American Psychological Association, 1–51. ISSN: 1939-1471 (1980).
47. McClelland, J. L., McNaughton, B. L. & O'Reilly, R. C. 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* **102.** Place: US Publisher: American Psychological Association, 419–457. ISSN: 1939-1471 (1995).
48. Mau, W., Hasselmo, M. E. & Cai, D. J. The brain in motion: How ensemble fluidity drives memory-updating and flexibility. *eLife* **9** (ed Colgin, L. L.) Publisher: eLife Sciences Publications, Ltd, e63550. ISSN: 2050-084X. `https://doi.org/10.7554/eLife.63550` (2024) (Dec. 2020).
49. Brinkman, B. A. W., Rieke, F., Shea-Brown, E. & Buice, M. A. Predicting how and when hidden neurons skew measured synaptic interactions. en. *PLOS Computational Biology* **14.** Publisher: Public Library of Science, e1006490. ISSN: 1553-7358. `https://journals.plos.org/ploscompbiol/article?id=10.1371/journal.pcbi.1006490` (2025) (Oct. 2018).
50. Cunningham, J. P. & Yu, B. M. Dimensionality reduction for large-scale neural recordings. en. *Nature Neuroscience* **17.** Publisher: Nature Publishing Group, 1500–1509. ISSN: 1546-1726. `https://www.nature.com/articles/nn.3776` (2025) (Nov. 2014).
51. Gallego, J. A., Perich, M. G., Miller, L. E. & Solla, S. A. Neural Manifolds for the Control of Movement. *Neuron* **94,** 978–984. ISSN: 0896-6273. `https://www.sciencedirect.com/science/article/pii/S0896627317304634` (2025) (June 2017).
52. Gallego, J. A. *et al.* Cortical population activity within a preserved neural manifold underlies multiple motor behaviors. en. *Nature Communications* **9.** Publisher: Nature Publishing Group, 4233. ISSN: 2041-1723. `https://www.nature.com/articles/s41467-018-06560-z` (2025) (Oct. 2018).
53. Rubin, A. *et al.* Revealing neural correlates of behavior without behavioral measurements. en. *Nature Communications* **10.** Publisher: Nature Publishing Group, 4745. ISSN: 2041-1723. `https://www.nature.com/articles/s41467-019-12724-2` (2025) (Oct. 2019).
54. Bauer, J. *et al.* Sensory experience steers representational drift in mouse visual cortex. en. *Nature Communications* **15.** Publisher: Nature Publishing Group, 9153. ISSN: 2041-1723. `https://www.nature.com/articles/s41467-024-53326-x` (2024) (Oct. 2024).
55. Delamare, G., Zaki, Y., Cai, D. J. & Clopath, C. Drift of neural ensembles driven by slow fluctuations of intrinsic excitability. *eLife* **12** (eds Giocomo, L. M. & Colgin, L. L.) Publisher: eLife Sciences Publications, Ltd, RP88053. ISSN: 2050-084X. `https://doi.org/10.7554/eLife.88053` (2024) (May 2024).
56. Kaufman, M. T., Churchland, M. M., Ryu, S. I. & Shenoy, K. V. Cortical activity in the null space: permitting preparation without movement. en. *Nature Neuroscience* **17.** Publisher: Nature Publishing Group, 440–448. ISSN: 1546-1726. `https://www.nature.com/articles/nn.3643` (2025) (Mar. 2014).

57. Rumpel, S. & Triesch, J. The dynamic connectome. en. *e-Neuroforum* **7,** 48–53. ISSN: 1868-856X. `https://doi.org/10.1007/s13295-016-0026-2` (2025) (Sept. 2016).

58. Kumaran, D., Hassabis, D. & McClelland, J. L. What Learning Systems do Intelligent Agents Need? Complementary Learning Systems Theory Updated. English. *Trends in Cognitive Sciences* **20.** Publisher: Elsevier, 512–534. ISSN: 1364-6613, 1879-307X. `https://www.cell.com/trends/cognitive-sciences/abstract/S1364-6613(16)30043-2` (2025) (July 2016).

59. Sweeney, Y. & Clopath, C. Population coupling predicts the plasticity of stimulus responses in cortical circuits. *eLife* **9** (eds Calabrese, R. L., Richards, B. A. & Doiron, B.) Publisher: eLife Sciences Publications, Ltd, e56053. ISSN: 2050-084X. `https://doi.org/10.7554/eLife.56053` (2025) (Apr. 2020).

60. Sheintuch, L. *et al.* Tracking the Same Neurons across Multiple Days in Ca2+ Imaging Data. English. *Cell Reports* **21.** Publisher: Elsevier, 1102–1115. ISSN: 2211-1247. `https://www.cell.com/cell-reports/abstract/S2211-1247(17)31430-4` (2025) (Oct. 2017).

61. Geva, N., Deitch, D., Rubin, A. & Ziv, Y. Time and experience differentially affect distinct aspects of hippocampal representational drift. English. *Neuron* **111.** Publisher: Elsevier, 2357–2366.e5. ISSN: 0896-6273. `https://www.cell.com/neuron/abstract/S0896-6273(23)00378-1` (2024) (Aug. 2023).

62. Howard, M. W. & Kahana, M. J. A Distributed Representation of Temporal Context. *Journal of Mathematical Psychology* **46,** 269–299. ISSN: 0022-2496. `https://www.sciencedirect.com/science/article/pii/S0022249601913884` (2023) (June 2002).

63. Etter, G., Manseau, F. & Williams, S. A Probabilistic Framework for Decoding Behavior From in vivo Calcium Imaging Data. *Frontiers in Neural Circuits* **14** (2020).

64. Yiu, A. P. *et al.* Neurons Are Recruited to a Memory Trace Based on Relative Neuronal Excitability Immediately before Training. en. *Neuron* **83,** 722–735. ISSN: 08966273. `https://linkinghub.elsevier.com/retrieve/pii/S089662731400628X` (2024) (Aug. 2014).

65. Rogerson, T. *et al.* Molecular and Cellular Mechanisms for Trapping and Activating Emotional Memories. en. *PLOS ONE* **11** (ed Sacktor, T. C.) e0161655. ISSN: 1932-6203. `https://dx.plos.org/10.1371/journal.pone.0161655` (2024) (Aug. 2016).

66. Chen, L. *et al.* The role of intrinsic excitability in the evolution of memory: Significance in memory allocation, consolidation, and updating. en. *Neurobiology of Learning and Memory* **173,** 107266. ISSN: 10747427. `https://linkinghub.elsevier.com/retrieve/pii/S1074742720301106` (2024) (Sept. 2020).

67. Sehgal, M., Ehlers, V. E. & Moyer, J. R. Synaptic and intrinsic plasticity within overlapping lateral amygdala ensembles following fear conditioning. *Frontiers in Cellular Neuroscience* **17,** 1221176. ISSN: 1662-5102. `https://www.frontiersin.org/articles/10.3389/fncel.2023.1221176/full` (2024) (Oct. 2023).

68. Hayashi, Y. NMDA Receptor-Dependent Dynamics of Hippocampal Place Cell Ensembles. en. *The Journal of Neuroscience* **39,** 5173–5182. ISSN: 0270-6474, 1529-2401. `https://www.jneurosci.org/lookup/doi/10.1523/JNEUROSCI.0243-19.2019` (2025) (June 2019).

69. Attardo, A., Fitzgerald, J. E. & Schnitzer, M. J. Impermanence of dendritic spines in live adult CA1 hippocampus. en. *Nature* **523.** Publisher: Nature Publishing Group, 592–596. ISSN: 1476-4687. `https://www.nature.com/articles/nature14467` (2024) (July 2015).

70. Pfeiffer, T. *et al.* Chronic 2P-STED imaging reveals high turnover of dendritic spines in the hippocampus in vivo. *eLife* **7** (ed Svoboda, K.) Publisher: eLife Sciences Publications, Ltd, e34700. ISSN: 2050-084X. `https://doi.org/10.7554/eLife.34700` (2024) (June 2018).

71. Sheffield, M. E. J. & Dombeck, D. A. Calcium transient prevalence across the dendritic arbour predicts place field properties. en. *Nature* **517.** Publisher: Nature Publishing Group, 200–204. ISSN: 1476-4687. `https://www.nature.com/articles/nature13871` (2024) (Jan. 2015).

72. Sheintuch, L., Geva, N., Deitch, D., Rubin, A. & Ziv, Y. Organization of hippocampal CA3 into correlated cell assemblies supports a stable spatial code. English. *Cell Reports* **42.** Publisher: Elsevier. ISSN: 2211-1247. `https://www.cell.com/cell-reports/abstract/S2211-1247(23)00130-4` (2024) (Feb. 2023).

73. Cai, D. J. *et al.* A shared neural ensemble links distinct contextual memories encoded close in time. en. *Nature* **534,** 115–118. ISSN: 0028-0836, 1476-4687. `https://www.nature.com/articles/nature17955` (2025) (June 2016).

74. Semiconscious. *File:HippocampalRegions.jpg - Wikimedia Commons* en. June 2006. `https://commons.wikimedia.org/wiki/File:HippocampalRegions.jpg` (2025).

75. Dong, C., Madar, A. D. & Sheffield, M. E. J. Distinct place cell dynamics in CA1 and CA3 encode experience in new environments. en. *Nature Communications* **12,** 2977. ISSN: 2041-1723. `https://www.nature.com/articles/s41467-021-23260-3` (2025) (May 2021).

76. Kemere, C., Carr, M. F., Karlsson, M. P. & Frank, L. M. Rapid and Continuous Modulation of Hippocampal Network State during Exploration of New Places. en. *PLoS ONE* **8** (ed Dickson, C. T.) e73114. ISSN: 1932-6203. `https://dx.plos.org/10.1371/journal.pone.0073114` (2025) (Sept. 2013).

77. Amaral, D. & Witter, M. The three-dimensional organization of the hippocampal formation: A review of anatomical data. en. *Neuroscience* **31,** 571–591. ISSN: 03064522. `https://linkinghub.elsevier.com/retrieve/pii/0306452289904247` (2025) (Jan. 1989).

78. Ishizuka, N., Weber, J. & Amaral, D. G. Organization of intrahippocampal projections originating from CA3 pyramidal cells in the rat. en. *Journal of Comparative Neurology* **295,** 580–623. ISSN: 0021-9967, 1096-9861. `https://onlinelibrary.wiley.com/doi/10.1002/cne.902950407` (2025) (May 1990).

79. Bezaire, M. J. & Soltesz, I. Quantitative assessment of CA1 local circuits: Knowledge base for interneuron-pyramidal cell connectivity: Quantitative Assessment Of Ca1 Local Circuits. en. *Hippocampus* **23,** 751–785. ISSN: 10509631. `https://onlinelibrary.wiley.com/doi/10.1002/hipo.22141` (2025) (Sept. 2013).

80. Nakashiba, T., Young, J. Z., McHugh, T. J., Buhl, D. L. & Tonegawa, S. Transgenic Inhibition of Synaptic Transmission Reveals Role of CA3 Output in Hippocampal Learning. en. *Science* **319,** 1260–1264. ISSN: 0036-8075, 1095-9203. `https://www.science.org/doi/10.1126/science.1151120` (2025) (Feb. 2008).

81. Nakazawa, K. *et al.* Hippocampal CA3 NMDA Receptors Are Crucial for Memory Acquisition of One-Time Experience. en. *Neuron* **38,** 305–315. ISSN: 08966273. `https://linkinghub.elsevier.com/retrieve/pii/S089662730300165X` (2025) (Apr. 2003).

82. Hainmueller, T. & Bartos, M. Parallel emergence of stable and dynamic memory engrams in the hippocampus. en. *Nature* **558.** Publisher: Nature Publishing Group, 292–296. ISSN: 1476-4687. `https://www.nature.com/articles/s41586-018-0191-2` (2025) (June 2018).

83. Leutgeb, J. K., Leutgeb, S., Moser, M.-B. & Moser, E. I. Pattern Separation in the Dentate Gyrus and CA3 of the Hippocampus. en. *Science* **315,** 961–966. ISSN: 0036-8075, 1095-9203. `https://www.science.org/doi/10.1126/science.1135801` (2025) (Feb. 2007).

84. Keinath, A. T., Nieto-Posadas, A., Robinson, J. C. & Brandon, M. P. DG–CA3 circuitry mediates hippocampal representations of latent information. en. *Nature Communications* **11.** Publisher: Nature Publishing Group, 3026. ISSN: 2041-1723. `https://www.nature.com/articles/s41467-020-16825-1` (2025) (June 2020).

85. Hubel, D. H. & Wiesel, T. N. Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. en. *The Journal of Physiology* **160,** 106–154. ISSN: 0022-3751, 1469-7793. `https://physoc.onlinelibrary.wiley.com/doi/10.1113/jphysiol.1962.sp006837` (2025) (Jan. 1962).

86. Wiesel, T. N. Postnatal development of the visual cortex and the influence of environment. eng. *Nature* **299,** 583–591. ISSN: 0028-0836 (Oct. 1982).

87. Ringach, D. L. *et al.* Spatial clustering of tuning in mouse primary visual cortex. en. *Nature Communications* **7.** Publisher: Nature Publishing Group, 12270. ISSN: 2041-1723. `https://www.nature.com/articles/ncomms12270` (2025) (Aug. 2016).

88. Ko, H., Mrsic-Flogel, T. D. & Hofer, S. B. Emergence of Feature-Specific Connectivity in Cortical Microcircuits in the Absence of Visual Experience. en. *Journal of Neuroscience* **34.** Publisher: Society for Neuroscience Section: Brief Communications, 9812–9816. ISSN: 0270-6474, 1529-2401. `https://www.jneurosci.org/content/34/29/9812` (2025) (July 2014).

89. Stone, J. V. *Vision and brain: how we perceive the world* eng. ISBN: 978-0-262-51773-7 (MIT press, Cambridge (Mass.), 2012).

90. Deitch, D., Rubin, A. & Ziv, Y. Representational drift in the mouse visual cortex. eng. *Current biology: CB* **31,** 4327–4339.e6. ISSN: 1879-0445 (Oct. 2021).

91. Logothetis, N. K. Vision: a window on consciousness. *Scientific American* **281,** 68–75. ISSN: 00368733, 19467087. `http://www.jstor.org/stable/26058485` (2025) (1999).

92. Töle, J. *File:mouse brain sagittal.svg* Mar. 2014. `https://commons.wikimedia.org/wiki/File:Mouse_brain_sagittal.svg`.

93. Ziv, Y. *et al.* Long-term dynamics of CA1 hippocampal place codes. en. *Nature Neuroscience* **16.** Publisher: Nature Publishing Group, 264–266. ISSN: 1546-1726. `https://www.nature.com/articles/nn.3329` (2024) (Mar. 2013).

94. Shani-Narkiss, H., Beniaguev, D., Segev, I. & Mizrahi, A. Stability and flexibility of odor representations in the mouse olfactory bulb. *Frontiers in Neural Circuits* **17,** 1157259. ISSN: 1662-5110. `https://www.ncbi.nlm.nih.gov/pmc/articles/PMC10157098/` (2025) (Apr. 2023).

95. Haberly, L. B. & Price, J. L. The axonal projection patterns of the mitral and tufted cells of the olfactory bulb in the rat. eng. *Brain Research* **129,** 152–157. ISSN: 0006-8993 (June 1977).

96. Padoa-Schioppa, C., Li, C.-S. R. & Bizzi, E. Neuronal activity in the supplementary motor area of monkeys adapting to a new dynamic environment. eng. *Journal of Neurophysiology* **91,** 449–473. ISSN: 0022-3077 (Jan. 2004).

97. Bliss, T. V. P. & Collingridge, G. L. A synaptic model of memory: long-term potentiation in the hippocampus. en. *Nature* **361,** 31–39. ISSN: 0028-0836, 1476-4687. `https://www.nature.com/articles/361031a0` (2024) (Jan. 1993).

98. Maffei, A. en. in *Oxford Research Encyclopedia of Neuroscience* (Oxford University Press, Feb. 2018). ISBN: 978-0-19-026408-6. https://oxfordre.com/neuroscience/view/10.1093/acrefore/9780190264086.001.0001/acrefore-9780190264086-e-148 (2024).

99. Nabavi, S. *et al.* Engineering a memory with LTD and LTP. en. *Nature* **511,** 348–352. ISSN: 0028-0836, 1476-4687. https://www.nature.com/articles/nature13294 (2024) (July 2014).

100. Hagena, H. & Manahan-Vaughan, D. Interplay of hippocampal long-term potentiation and long-term depression in enabling memory representations. *Philosophical Transactions of the Royal Society B: Biological Sciences* **379.** Publisher: Royal Society, 20230229. https://royalsocietypublishing.org/doi/10.1098/rstb.2023.0229 (2024) (June 2024).

101. Micou, C. & O'Leary, T. Representational drift as a window into neural and behavioural plasticity. *Current Opinion in Neurobiology* **81,** 102746. ISSN: 0959-4388. https://www.sciencedirect.com/science/article/pii/S0959438823000715 (2024) (Aug. 2023).

102. Migliore, M., De Simone, G. & Migliore, R. Effect of the initial synaptic state on the probability to induce long-term potentiation and depression. eng. *Biophysical Journal* **108,** 1038–1046. ISSN: 1542-0086 (Mar. 2015).

103. Alam, M. J. *et al.* Adult Neurogenesis Conserves Hippocampal Memory Capacity. en. *The Journal of Neuroscience* **38,** 6854–6863. ISSN: 0270-6474, 1529-2401. https://www.jneurosci.org/lookup/doi/10.1523/JNEUROSCI.2976-17.2018 (2025) (Aug. 2018).

104. Gonçalves, J. T., Schafer, S. T. & Gage, F. H. Adult Neurogenesis in the Hippocampus: From Stem Cells to Behavior. *Cell* **167,** 897–914. ISSN: 0092-8674. https://www.sciencedirect.com/science/article/pii/S0092867416314040 (2025) (Nov. 2016).

105. Gage, F. H. Adult Neurogenesis in the Human Dentate Gyrus. en. *Hippocampus* **35.** _eprint: https://onlinelibrary.wiley.c e23655. ISSN: 1098-1063. https://onlinelibrary.wiley.com/doi/abs/10.1002/hipo.23655 (2025) (2025).

106. Kempermann, G. *et al.* Human Adult Neurogenesis: Evidence and Remaining Questions. *Cell Stem Cell* **23,** 25–30. ISSN: 1934-5909. https://www.sciencedirect.com/science/article/pii/S1934590918301668 (2025) (July 2018).

107. Richards, B. A. & Frankland, P. W. The Persistence and Transience of Memory. en. *Neuron* **94,** 1071–1084. ISSN: 08966273. https://linkinghub.elsevier.com/retrieve/pii/S0896627317303653 (2025) (June 2017).

108. Srivastava, N., Hinton, G., Krizhevsky, A., Sutskever, I. & Salakhutdinov, R. Dropout: a simple way to prevent neural networks from overfitting. *J. Mach. Learn. Res.* **15,** 1929–1958. ISSN: 1532-4435 (Jan. 2014).

109. Aitken, K., Garrett, M., Olsen, S. & Mihalas, S. The geometry of representational drift in natural and artificial neural networks. en. *PLOS Computational Biology* **18** (ed Latham, P. E.) e1010716. ISSN: 1553-7358. https://dx.plos.org/10.1371/journal.pcbi.1010716 (2024) (Nov. 2022).

110. Duque, A. & Spector, R. A Balanced Evaluation of the Evidence for Adult Neurogenesis in Humans: Implication for Neuropsychiatric Disorders. *Brain structure & function* **224,** 2281–2295. ISSN: 1863-2653. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6852840/ (2025) (Sept. 2019).

111. Nano, P. R. & Bhaduri, A. Mounting evidence suggests human adult neurogenesis is unlikely. *Neuron* **110,** 353–355. ISSN: 0896-6273. https://www.sciencedirect.com/science/article/pii/S0896627322000046 (2025) (Feb. 2022).

112. Sorrells, S. F. *et al.* Human hippocampal neurogenesis drops sharply in children to undetectable levels in adults. en. *Nature* **555.** Publisher: Nature Publishing Group, 377–381. ISSN: 1476-4687. `https://www.nature.com/articles/nature25975` (2025) (Mar. 2018).

113. Boldrini, M. *et al.* Human Hippocampal Neurogenesis Persists throughout Aging. eng. *Cell Stem Cell* **22,** 589–599.e5. ISSN: 1875-9777 (Apr. 2018).

114. Abbott, L. C. & Nigussie, F. Adult neurogenesis in the mammalian dentate gyrus. en. *Anatomia, Histologia, Embryologia* **49.** _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/ahe.12496, 3–16. ISSN: 1439-0264. `https://onlinelibrary.wiley.com/doi/abs/10.1111/ahe.12496` (2025) (2020).

115. Benarroch, E. E. Adult neurogenesis in the dentate gyrus. *Neurology* **81.** Publisher: Wolters Kluwer, 1443–1452. `https://www.neurology.org/doi/abs/10.1212/WNL.0b013e3182a9a156` (2025) (Oct. 2013).

116. Ziv, N. E. & Brenner, N. Synaptic Tenacity or Lack Thereof: Spontaneous Remodeling of Synapses. English. *Trends in Neurosciences* **41.** Publisher: Elsevier, 89–99. ISSN: 0166-2236, 1878-108X. `https://www.cell.com/trends/neurosciences/abstract/S0166-2236(17)30237-0` (2024) (Feb. 2018).

117. Devalle, F., Zou, L., Cecchini, G. & Roxin, A. *Representational drift as the consequence of ongoing memory storage* en. June 2024. `http://biorxiv.org/lookup/doi/10.1101/2024.06.25.600729` (2024).

118. Yasumatsu, N., Matsuzaki, M., Miyazaki, T., Noguchi, J. & Kasai, H. Principles of Long-Term Dynamics of Dendritic Spines. en. *Journal of Neuroscience* **28.** Publisher: Society for Neuroscience Section: Articles, 13592–13608. ISSN: 0270-6474, 1529-2401. `https://www.jneurosci.org/content/28/50/13592` (2024) (Dec. 2008).

119. Minerbi, A. *et al.* Long-Term Relationships between Synaptic Tenacity, Synaptic Remodeling, and Network Activity. en. *PLOS Biology* **7.** Publisher: Public Library of Science, e1000136. ISSN: 1545-7885. `https://journals.plos.org/plosbiology/article?id=10.1371/journal.pbio.1000136` (2024) (June 2009).

120. Stettler, D. D., Yamahachi, H., Li, W., Denk, W. & Gilbert, C. D. Axons and Synaptic Boutons Are Highly Dynamic in Adult Visual Cortex. English. *Neuron* **49.** Publisher: Elsevier, 877–887. ISSN: 0896-6273. `https://www.cell.com/neuron/abstract/S0896-6273(06)00135-8` (2025) (Mar. 2006).

121. Grillo, F. W. *et al.* Increased axonal bouton dynamics in the aging mouse cortex. en. *Proceedings of the National Academy of Sciences* **110.** ISSN: 0027-8424, 1091-6490. `https://pnas.org/doi/full/10.1073/pnas.1218731110` (2025) (Apr. 2013).

122. Zuo, Y., Lin, A., Chang, P. & Gan, W.-B. Development of Long-Term Dendritic Spine Stability in Diverse Regions of Cerebral Cortex. en. *Neuron* **46,** 181–189. ISSN: 08966273. `https://linkinghub.elsevier.com/retrieve/pii/S0896627305003090` (2025) (Apr. 2005).

123. Squire, L. R. Memory and the hippocampus: a synthesis from findings with rats, monkeys, and humans. eng. *Psychological Review* **99,** 195–231. ISSN: 0033-295X (Apr. 1992).

124. Dudai, Y., Karni, A. & Born, J. The Consolidation and Transformation of Memory. en. *Neuron* **88,** 20–32. ISSN: 08966273. `https://linkinghub.elsevier.com/retrieve/pii/S0896627315007618` (2025) (Oct. 2015).

125. Teyler, T. J. & DiScenna, P. The hippocampal memory indexing theory. en. *Behavioral Neuroscience* **100,** 147–154. ISSN: 1939-0084, 0735-7044. `https://doi.apa.org/doi/10.1037/0735-7044.100.2.147` (2025) (1986).

126. Teyler, T. J. & Rudy, J. W. The hippocampal indexing theory and episodic memory: updating the index. eng. *Hippocampus* **17,** 1158–1169. ISSN: 1050-9631 (2007).

127. Nadel, L. & Moscovitch, M. Memory consolidation, retrograde amnesia and the hippocampal complex. en. *Current Opinion in Neurobiology* **7,** 217–227. ISSN: 09594388. `https://linkinghub.elsevier.com/retrieve/pii/S0959438897800104` (2025) (Apr. 1997).

128. Nadel, L., Samsonovich, A., Ryan, L. & Moscovitch, M. Multiple trace theory of human memory: Computational, neuroimaging, and neuropsychological results. en. *Hippocampus* **10,** 352–368. ISSN: 1050-9631, 1098-1063. `https://onlinelibrary.wiley.com/doi/10.1002/1098-1063(2000)10:4%3C352::AID-HIPO2%3E3.0.CO;2-D` (2025) (2000).

129. Kolibius, L. D., Josselyn, S. A. & Hanslmayr, S. On the origin of memory neurons in the human hippocampus. *Trends in Cognitive Sciences* **29,** 421–433. ISSN: 1364-6613. `https://www.sciencedirect.com/science/article/pii/S1364661325000312` (2025) (May 2025).

130. Petraki, E., Idreos, S. & Manegold, S. *Holistic Indexing in Main-memory Column-stores* en. in *Proceedings of the 2015 ACM SIGMOD International Conference on Management of Data* (ACM, Melbourne Victoria Australia, May 2015), 1153–1166. ISBN: 978-1-4503-2758-9. `https://dl.acm.org/doi/10.1145/2723372.2723719` (2025).

131. Logothetis, N. K. *et al.* Hippocampal–cortical interaction during periods of subcortical silence. en. *Nature* **491.** Publisher: Nature Publishing Group, 547–553. ISSN: 1476-4687. `https://www.nature.com/articles/nature11618` (2025) (Nov. 2012).

132. Khodagholy, D., Gelinas, J. N. & Buzsáki, G. Learning-enhanced coupling between ripple oscillations in association cortices and hippocampus. *Science* **358.** Publisher: American Association for the Advancement of Science, 369–372. `https://www.science.org/doi/10.1126/science.aan6203` (2025) (Oct. 2017).

133. Buzsáki, G. Hippocampal sharp wave-ripple: A cognitive biomarker for episodic memory and planning. *Hippocampus* **25,** 1073–1188. ISSN: 1050-9631. `https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4648295/` (2025) (Oct. 2015).

134. Dragoi, G. & Tonegawa, S. Preplay of future place cell sequences by hippocampal cellular assemblies. en. *Nature* **469,** 397–401. ISSN: 0028-0836, 1476-4687. `https://www.nature.com/articles/nature09633` (2025) (Jan. 2011).

135. Dragoi, G. & Tonegawa, S. Selection of preconfigured cell assemblies for representation of novel spatial experiences. en. *Philosophical Transactions of the Royal Society B: Biological Sciences* **369,** 20120522. ISSN: 0962-8436, 1471-2970. `https://royalsocietypublishing.org/doi/10.1098/rstb.2012.0522` (2025) (Feb. 2014).

136. Maboudi, K., Giri, B., Miyawaki, H., Kemere, C. & Diba, K. Retuning of hippocampal representations during sleep. *Nature* **629,** 630–638. ISSN: 0028-0836. `https://www.ncbi.nlm.nih.gov/pmc/articles/PMC11472358/` (2025) (May 2024).

137. Ghandour, K. *et al.* Parallel processing of past and future memories through reactivation and synaptic plasticity mechanisms during sleep. en. *Nature Communications* **16.** Publisher: Nature Publishing Group, 3618. ISSN: 2041-1723. `https://www.nature.com/articles/s41467-025-58860-w` (2025) (Apr. 2025).