



Hippocampal and cortical contributions to statistical learning

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The human brain is adept at extracting regularities from our environment, allowing us to behave adaptively and make predictions. Research on the neural basis of this statistical learning has diverged in recent years based on the brain mechanism being investigated and the timing and modality of the regularities. One literature has focused on the entrainment of neural oscillations to rapid auditory sequences in cortical regions. The other literature has focused on changes in the similarity of neural representations for slower visual sequences in the hippocampus. By reuniting these literatures, we identify a potential role for the hippocampus in generalizing over temporal variability and suggest how hippocampal-cortical interactions could support statistical learning.

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Introduction

Life is full of rich, complex, and novel experiences, which are grounded in the structure of the environment. Acquiring this underlying structure through statistical learning (SL) scaffolds how we represent and remember these experiences and how we interact with the world efficiently going forward. Here, we focus on the neural mechanisms involved in the automatic and often implicit extraction of a subset of environmental regularities, namely repeated patterns in experience across time (temporal regularities) on the scale of minutes to hours—an SL ability that exists throughout our lifespan.

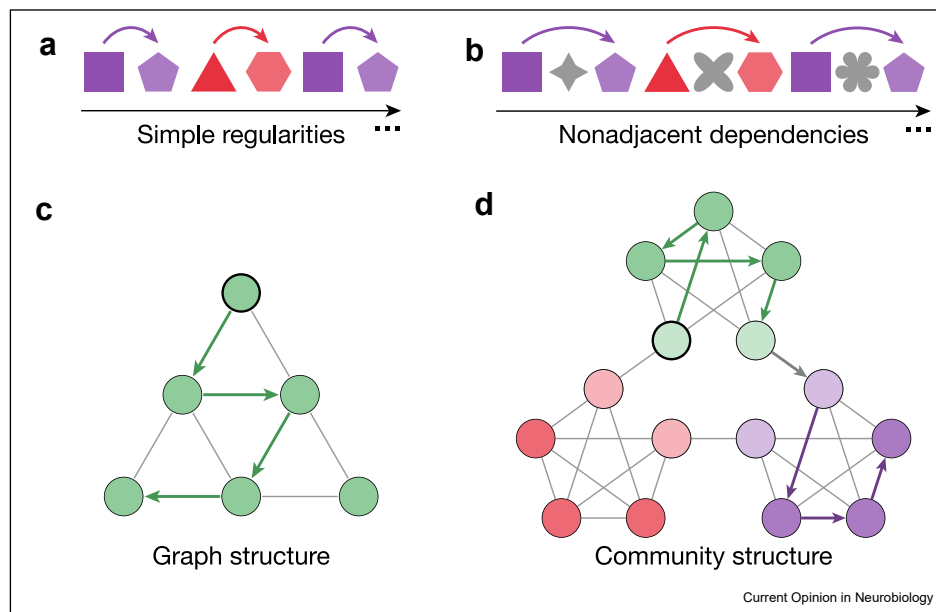
Temporal regularities can take various forms. Specific experiences may co-occur frequently in a particular order (e.g., short sequences of syllables forming words), producing simple regularities of items grouped into discrete sequential units [1] ([Figure 1a](#)). Learning these simple regularities is thought to rely on sensitivity to transition probabilities (TPs)—the probability of a stimulus given the prior stimulus, which is higher within units than across—as well as the ability to segment continuous experience into meaningful chunks [2]. More complex regularities can extend or isolate these mechanisms. For example, co-occurring experiences may be interrupted by unrelated items, producing nonadjacent dependencies and longer-range relationships [3] ([Figure 1b](#)). Alternatively, random walks between states in graph structures can generate sequences of experiences that lack clear points of segmentation but retain informative TPs [4] ([Figure 1c](#)). Graphs can also produce sequences with hierarchical structure, wherein TPs are uninformative but experiences can nevertheless be segmented at boundaries between interconnected communities of states [5] ([Figure 1d](#)).

Recently, SL of simple regularities has been investigated in two diverging lines of research, based on different theories of the underlying neural mechanisms. In one line, stimuli are presented rapidly and SL is measured in terms of neural synchrony in scalp electroencephalography (EEG) or magnetoencephalography (MEG), which primarily capture cortical signals. In the other line, stimuli are presented slowly and/or asynchronously and SL is measured in terms of the amplitude and spatial patterns of neural responses with functional magnetic resonance imaging (fMRI), often focusing on the hippocampus. Below, we draw connections between these two literatures and expose potential unifying directions for future research.

Neural measures of statistical learning

Several brain regions have been linked to SL. The inferior frontal gyrus (IFG), which plays a domain-general role in a variety of cognitive functions [6], is involved in SL across modalities, showing enhanced activation for structured sequences of syllables [7], tones [8], and shapes [9]. The superior temporal gyrus

Figure 1



Types of statistical learning. (a) Simple regularities. Items are grouped into units (commonly pairs or triplets), with a higher transition probability (TP) between items within a unit than between items that span units. This variation in TPs enables segmentation of discrete units from continuous input. (b) Nonadjacent dependencies. Co-occurring items are separated by unrelated intervening items, which requires learning patterns beyond pairwise TPs. (c) Graph structure. Items appear as nodes on a graph, with related pairs of items connected by a bidirectional or directed edge. An item has equal probability of transitioning to any of its directly connected nodes. The hidden graph structure is learned incidentally through exposure to sequences generated via walks along the graph. (d) Community structure. A type of graph structure in which groups of items occur in interconnected communities. Random walks along this structure generate a series of within-community subsequences bounded by transitions to new communities. Critically, the TPs for edges within versus across communities are matched, and thus community membership is defined instead by the overlap of potential transitions from a given node.

(STG), which is highly sensitive to speech sounds and features [10,11], is commonly implicated in auditory SL, particularly for linguistic structure [7]. The hippocampus, which contributes to learning and memory by forming rapid associations [12], shows increased activity [9,13], representational changes [14], and predictive responses [15] as a result of visual SL.

Online neural entrainment to rapid regularities

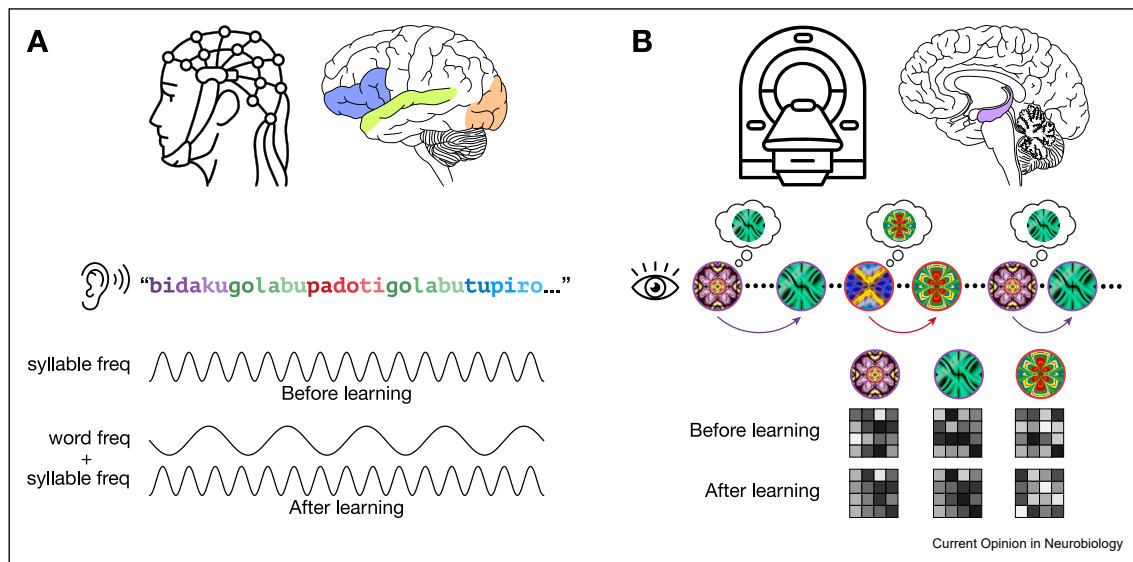
Early studies suggested that SL may be a key factor in language development by demonstrating that preverbal infants could use temporal regularities to segment arbitrary ‘words’ from continuous streams of spoken syllables [1]. Subsequent studies introduced variations on this canonical design, including nonspeech sounds [16] and words [17], as well as visual stimuli such as shapes [1] and faces [18] to construct pairs, triplets, or larger segmented units [19].

Rhythmic entrainment to rapid continuous stimulus streams has emerged as an online measure of SL that can be used to track the time course of learning; this stands in contrast to traditional offline measures of SL that are obtained in a separate test phase. In entrainment designs, participants come to experience the continuous

stream as structured units (e.g. words) rather than as individual items (e.g. syllables), even though this segmentation is fully constructed by their mind through learning. Such learned segmentation appears in EEG recordings as an increase in the power and/or coherence of neural oscillations at the frequency of the word boundaries, in addition to persistent oscillations at the frequency of individual syllables driven by the acoustics of the input stream [20] (Figure 2a). Entrainment to word-level frequencies suggests successful chunking of syllables into structured word units, though the underlying mechanisms driving entrainment remain unclear [21]. Crucially, entrainment measures require stimuli to be presented rapidly at a stationary rate but are simple to administer across populations and without overt task demands.

EEG entrainment to auditory syllable triplets—occurring maximally among centrofrontal electrodes—predicts postlearning behavioral performance in implicit [22] and explicit word recognition tests [23] (for a review, see Ref. [21]). In MEG, cortical entrainment to tone triplets [24] and word pairs [25] predicts performance on explicit behavioral tests. These effects are found robustly at the group level [26] and have increasingly been used to detect

Figure 2



Two lines of SL research. (a) EEG/MEG studies of SL commonly use word-learning paradigms consisting of continuous, rhythmic speech streams containing hidden syllable triplets. Cortical oscillations measured from the scalp entrain to the frequency of individual syllables throughout learning but additionally begin to entrain to the frequency of the learned words (i.e. $\frac{1}{3}$ of the syllable frequency) within a few minutes of exposure, indicating that the 'words' may now be perceived as units [20]. (b) fMRI studies of SL often involve exposure to continuous visual streams containing hidden pairs of stimuli (e.g. fractals) with slower, variable timing between items. Hippocampal activity patterns evoked by the paired stimuli, presented on their own in a random order before and after learning, become more similar to each other, indicating that the representations of these items have integrated [14]. EEG, electroencephalography; fMRI, functional magnetic resonance imaging; MEG, magnetoencephalography; SL, statistical learning.

SL in populations for whom behavioral testing is difficult. In preverbal infants, for example, the time course over which entrainment emerges during auditory word learning matches that of adults [27]. Entrainment to regularities has also been demonstrated in sleeping newborns [28,29] and in patients in minimally conscious states [30] and has been proposed as a clinical tool for determining the diagnosis and prognosis of patients with disorders of consciousness [31,32]. One challenge is that the sensitivity and reliability of entrainment at the individual level is uncertain [26].

Offline integration of slow regularities

A distinct group of studies, primarily using fMRI, has sought to characterize SL as the representational integration of temporally associated items. After exposure to temporal regularities, distributed patterns of neural activation become more similar for items within the same learned unit than for items across different units. Because of the slow hemodynamic response, many fMRI studies of SL use event-related task designs with longer stimulus presentations and jittered interstimulus intervals (ISIs) spanning multiple seconds. In addition, because fMRI data are susceptible to temporal auto-correlation, studies are commonly structured with prelearning and postlearning runs containing no statistical regularities that can be used to take representational snapshots. SL is then assessed by evaluating

changes in representational similarity from prelearning to postlearning (Figure 2b).

Neural integration from SL has primarily been detected in the hippocampus and surrounding medial temporal lobe (MTL) cortices. For example, after viewing a sequence of abstract visual fractals with embedded temporal pairs, fractals from pairs that had high TPs showed increased pattern similarity in the hippocampus, parahippocampal cortex (PHC), and perirhinal cortex [14]. These changes were asymmetric, with the first item in a pair evoking the second item's pattern more than the reverse, consistent with a predictive representation. Indeed, after learning a sequence of scenes that were trial-unique but contained category-level pairs (e.g. beaches were always followed by mountains), neural representations in the hippocampus (but not visual cortex or PHC) came to reflect the upcoming scene category [15].

In related work, exposure to a sequence of objects derived from a random walk on a graph led to fMRI adaptation in the hippocampus and entorhinal cortex (EC) proportional to the associative distances between nodes on the graph [5,33]. The hippocampus supports similar predictive [34] and hierarchical [35] representations during associative and sequence learning paradigms.

SL does not always lead to the integration of associated items and in fact can lead to the opposite—reduced representational similarity or differentiation. This has been observed when pairs have lower TPs [14], when learned pair structure is violated [36], or when paired stimuli start off with moderately high visual similarity [37]. These results can be accounted for by the nonmonotonic plasticity hypothesis, whereby differentiation occurs as a result of moderate competition between memories [38].

Bridging the gap between entrainment and representation

There are many differences between studies of online entrainment and offline integration: neuroimaging technique, stimulus speed and rhythmicity, stimulus modality, and anatomical basis (Figure 2). Typically, studies using EEG/MEG explore online entrainment effects in a rapid and continuous form of SL, whereas studies using fMRI focus on the offline integrative consequences of learning slow, often temporally variable SL. Entrainment effects are found primarily in cortical regions during auditory tasks, whereas integration effects are found primarily in the hippocampus during visual tasks. Studies sharing characteristics across both lines of research may help to bridge these differences.

Relationship between cortical and hippocampal processes

Intracranial electroencephalography (iEEG) studies have started to reveal integration in cortical regions beyond the MTL. One iEEG study of SL for scene category pairs found that the visual cortex not only represents the currently perceived image category but also predicts the upcoming category [39]. In contrast, a similar fMRI study found predictive effects only in the hippocampus and not in the PHC or visual cortex [15]. Sensory cortical areas may show enhanced engagement during online learning (as measurable with iEEG) while regularities are intact, compared with the unstructured and delayed presentation of items in postlearning runs (as commonly used in fMRI). The transience of the cortical prediction effect—in the short period between a predictive and predicted item [39]—also makes it difficult to detect with slow hemodynamic measures, though this issue can be circumvented by occasionally omitting predicted stimuli [34,40,41]. Beyond SL paradigms, representations of predicted visual stimuli have been decoded from the visual cortex [34] and expectation-based increases in visual cortical activity have been found in infants as young as 6 months old [42].

Cortical entrainment to regularities may also reflect multiple aspects of learning, including predictive signals. In iEEG experiments of SL for both visual pairs and auditory triplets, cortical electrodes that entrain

exclusively to the learned word frequency also code for ordinal position of items within the word (with earlier items being predictive and later items being predictable), whereas cortical electrodes that entrain to both the word and its constituent syllables code for TPs [43]. Evidence for whether the entrainment observed in cortex also occurs in the hippocampus is mixed. One iEEG study failed to find entrainment in the hippocampus for auditory or visual modalities [43] but did find representational integration there (see also [44]). Another iEEG study did detect a power spectrum peak in the hippocampus at the learned word frequency during an auditory SL task [45].

These overlapping effects of SL in the hippocampus and cortex raise the question of how these two systems interact. One possibility is that hippocampal integration is necessary for both SL and cortical entrainment across modalities. Indeed, patients with bilateral hippocampal lesions show impairment in visual and auditory SL of pair and triplet structures [46] and direct electrical stimulation of the hippocampus impairs visual SL [47]. Moreover, recent evidence suggests that predictive representations are communicated from the hippocampus to cortical regions. Cue-outcome integration in the hippocampus is associated with subsequent predictive representations in visual cortex [34], and predictive representations are communicated via a feedback connection from hippocampal subfield CA2/3 to the deep layers of the PHC [48]. By this view, cortical effects such as entrainment and prediction may emerge as consequences of ‘word’ representations learned in the hippocampus.

Another possibility is that cortical entrainment proceeds independently of representational changes in the hippocampus. Indeed, the presence of hippocampal integration effects in temporally varied sequences that are incompatible with entrainment suggests that the two neural measures of SL are dissociable. Moreover, selectively modulating entrainment to auditory word frequencies via rhythmic visual stimulation can accelerate SL [49], which is inconsistent with cortical entraining being a byproduct. Given that entrainment emerges rapidly during SL [20], it is also possible that cortical entrainment helps drive hippocampal integration by highlighting the presence of fast, rhythmic regularities in an input stream or by facilitating the detection of boundaries between which stimuli can be integrated. The time course of hippocampal integration effects remains an open question.

Measuring cortical entrainment in patients with bilateral hippocampal loss or during bilateral stimulation in iEEG would help reconcile these accounts. If entrainment is still observed, cortical regions may support SL mechanisms without hippocampal involvement. Ultimately, the relationship between hippocampal and

cortical processes, as well as their roles in SL, may depend on the timing and content of statistical regularities.

Temporal scale and rhythmicity

Differences in task timing between the two literatures arose from technical considerations: relatively fast and rhythmic stimuli are required for entrainment in EEG/MEG, whereas slower and jittered trials are required to deconvolve hemodynamic responses in fMRI. Nevertheless, this distinction may be important for characterizing the role of the hippocampus. Across many cognitive domains, introducing delays engages hippocampal learning. In classical conditioning, for example, the hippocampus plays a necessary role when the conditioned stimulus and unconditioned stimulus are separated by a gap in time (i.e. trace conditioning) but not when they are presented contiguously (i.e. delay conditioning) [50]. The hippocampus is similarly recruited in reinforcement learning when feedback is delayed [51].

Single-unit recordings in the human brain have started to bridge the gap between online and offline measures of SL without the need for rhythmicity. Namely, these recordings combine the temporal precision of EEG/MEG (which allows for online measures without needing offline prelearning/postlearning snapshots) with the spatial precision of fMRI (which allows for localization to the hippocampus). During exposure to a sequence of face images generated using a random walk along a graph structure, a subset of neurons in the hippocampus and EC that initially responded to specific faces gradually increased their response to other nonpreferred images that were connected directly (but not indirectly) in the graph, demonstrating neuron-level sensitivity to TPs [44].

Crucially, this study adopted a task design inspired by fMRI studies of visual SL [14,5], including slow stimulus presentation, a jittered ISI of 1–3 s, and prelearning and postlearning snapshot phases with no regularities. Reliance on unstructured postlearning runs in fMRI studies has left open questions about whether hippocampal representations of individual stimuli accurately reflect representations during learning, given that hippocampal activity patterns can change rapidly when learned predictions are violated (in this case, during the randomly ordered postlearning phase) [36]. However, the aforementioned single-unit study observed similar results between online learning and offline postlearning phases [44].

Content domains

In addition to differences in the timing of stimulus presentation, these literatures also focus on different types of stimuli: studies of entrainment often use

linguistic auditory stimuli (e.g. syllables or words), while studies of representational change typically use nonlinguistic visual stimuli (e.g. scenes, faces, fractals). These practices are consistent with natural temporal constraints occurring in these content domains: linguistic auditory SL operates best at faster stimulus presentation rates, whereas nonlinguistic visual SL benefits from slower rates [52,18]. This raises the possibility that the hippocampus and cortex contribute to SL for distinct content domains.

Sensory modality

Although entrainment and representational change are often assessed in auditory and visual modalities, respectively, these measures are not inherently modality-specific. In particular, visual SL can induce entrainment in cortical regions sensitive to visual features: in scalp EEG, word-level entrainment occurs in frontocentral and parieto-occipital regions during visual learning of written syllable triplets [53]; in iEEG, entrainment to pairs of scene exemplars or categories has been observed across frontal and sensory cortices [54,39], as well as to pairs of fractals in anterior frontal, parietal, and temporal cortices [43].

Rapid and rhythmic auditory regularities can also undergo representational change. Although modality-specific areas such as the STG only represent low-level statistical features like pairwise TPs between auditory stimuli, supramodal regions such as the IFG and hippocampus code for higher-level statistics in both auditory and visual modalities by developing more similar representations for stimuli belonging to the same statistical unit [43]. It remains an open question whether these auditory representations are predictive like those found in fMRI studies of visual SL and whether auditory SL remains intact during the slower, temporally varied task designs commonly used in fMRI. Different temporal constraints across SL modalities [52] may pose a methodological challenge for such investigations. Given that temporal scale and rhythmicity may affect the role of the hippocampus, these constraints also introduce the possibility that hippocampal involvement in slower, temporally varied SL is modulated by sensory modality.

Linguistic relevance

Task stimuli can additionally be divided into linguistic (e.g. syllables) and nonlinguistic (e.g. tones) regularities. Linguistic auditory SL exhibits a unique developmental trajectory, improving during infancy [18] and stabilizing by early childhood [55], whereas nonlinguistic auditory SL is present early [1] but continues to develop between 5 and 12 years of age [56]. Linguistic and nonlinguistic forms of auditory SL also activate largely nonoverlapping cortical regions in 5- to 7-year-old

children [57]. Cortical activation in linguistic auditory SL overlaps with the language network in posterior temporal gyrus [58], whereas the hippocampus is inconsistently engaged by linguistic auditory SL and may be more sensitive to nonlinguistic regularities [7,57,58]. At the same time, visual regularities can be learned in newborns [59] and throughout infancy [60], and they evoke hippocampal activation in preverbal infants as young as 3 months [13]. Autism spectrum disorder, which is known to affect language development, also selectively impairs linguistic SL (but not nonlinguistic SL) in both auditory and visual modalities during childhood [61].

This evidence suggests that speech is a privileged target for SL that may rely less on the hippocampus than other modalities. SL has been suggested to be specifically adapted for language acquisition, which poses a unique evolutionary advantage in humans [62]. However, the linguistic relevance of auditory stimuli alone does not confer an SL advantage: perceiving ambiguous auditory stimuli (i.e. sine-wave speech) as speech or nonspeech does not affect the ability to extract patterns [16]. Nevertheless, temporal constraints on nonlinguistic auditory stimuli are not well understood, which presents a possible avenue for relating neural mechanisms across sensory modalities (e.g. if SL for such auditory stimuli can operate at the slower and more variable presentation often used for visual stimuli).

Prior knowledge

Pre-experimental knowledge may account for the unique behavioral and neural characteristics of linguistic auditory SL. In linguistic auditory word-learning paradigms, knowledge about syllable co-occurrence in a native language facilitates learning of related artificial words, leading to inconsistent learning for words within the same task [63,64]. Performance on paradigms affected by prior knowledge is also unreliable upon retest [65] and uncorrelated with matched tasks in other modalities [66]. In contrast, visual and nonlinguistic auditory paradigms with abstract stimuli that are less subject to strong prior knowledge exhibit consistent learning across structures and modalities [63]. Visual SL is also enhanced when individual stimuli are simple and familiar [67].

Focusing on prior knowledge may also help disentangle when and how the hippocampus is expected to be involved in SL. During the learning process, the hippocampus detects prediction errors and preferentially represents prediction-violating stimuli [68]; once learning is complete, however, the hippocampus represents predicted information regardless of what is being perceived and whether it matches the prediction. Thus, significant prior knowledge about regularities in a domain (e.g. syllable co-occurrences in a native language) may trigger pre-existing predictive signals that obscure hippocampal

Box 1. Theoretical models of statistical learning

The two literatures reviewed here have been linked to different theories about the neural mechanisms that underlie SL. One theory proposes that SL is supported primarily by input-driven, automatic, and modality-specific mechanisms in the cortex [69,70]. Indeed, simple Hebbian learning models—imitating general cortical plasticity—can account for pair and triplet SL [71] and generate characteristic rhythmic entrainment effects [72]. According to this view, cortical mechanisms are sufficient for SL, while the hippocampus supports parallel but nonessential memory processes [73].

Alternative theories posit a central and necessary role for the hippocampus in SL. One neural network model suggests that the hippocampus supports both episodic memory and SL via different circuit pathways [74]. In the trisynaptic pathway (TSP)—connecting the EC to hippocampal subfields dentate gyrus (DG), CA3, and CA1—high inhibition and a fast learning rate lead to the sparse representations and pattern separation needed for episodic memory. In the monosynaptic pathway (MSP)—a direct, recurrent connection between EC and CA1—lower inhibition and a slower learning rate lead to overlapping representations of related experiences, reinforcing their regularities gradually in support of SL. This model successfully acquires temporal regularities from EC input and develops integrated representations of paired stimuli in CA1, which remain intact after a simulated lesion of the TSP. This is consistent with experimental evidence that SL persists in populations where the TSP is underdeveloped or impaired compared to the MSP, such as infants [13] and patients with selective DG lesions [75]. Given that the TSP and MSP share common subfields in CA1 and in the EC input and output layers, this model also raises questions about how and when SL and episodic memory compete (or cooperate) [15] and how this interaction is modulated by the differential effects of stress on hippocampal subfields [76].

SL of graph structures [4,5,33,44] (Figure 1c), which does not depend on deterministic transitions or segmented words, is commonly attributed to hippocampal successor representations [77]. In this framework, hippocampal neurons form predictive representations of possible upcoming states. Thus, learned representations of graph structures are distorted such that nodes along commonly traversed paths have more similar representations. This model places SL in a broader literature involving the construction of abstract cognitive maps for optimal decision-making and reinforcement learning [78].

Although these theorized mechanisms all do a good job accounting for SL of simple regularities, they may differ in their ability to explain SL of complex regularities thought to rely on similar mechanisms [79]. Nonadjacent dependencies (Figure 1b) can be successfully captured in simple Hebbian models [80] and are a key aspect of the successor representation [78]. On the other hand, the hippocampal pathway model accounts for the acquisition of distributional structure. This includes category learning [81] and structure learning [74] (Figure 1d), in which items grouped into temporal communities exhibit high within-group representational similarity [5,82,83]. It remains to be determined whether SL of different types of regularities and content domains requires different models or mechanisms or whether these tasks can be subsumed in enriched versions of current models.

responses to certain regularities that are novel to the task. Future studies could test for increased hippocampal

involvement in auditory SL for complex, unfamiliar stimuli (e.g., auditory objects or scenes) and introduce violations to distinguish between stages of learning.

Conclusions

We have identified two threads of SL research focusing on distinct brain regions, time scales, and sensory modalities, and we have explored existing and future evidence that could bridge this divide. In the process, we have also revealed underexplored areas of interest, including clarifying the role of the hippocampus in SL and its interactions with cortical mechanisms (see also Box 1). We suggest that the hippocampus may be necessary for SL during slower and temporally variable sequences and/or when stimuli are unfamiliar. In this way, the hippocampus may generalize over temporal noise to extract novel patterns of experience that guide how we represent, remember, and interact with the world.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

No data were analyzed for this review article.

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Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

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