Trends in Cognitive Sciences

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Review

# Boundaries Shape Cognitive Representations of Spaces and Events

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**Efficient navigation from one place to another is facilitated by the ability to use spatial boundaries to segment routes into their component parts. Similarly, memory for individual episodes relies on the ability to use shifts in spatiotemporal contexts to segment the ongoing stream of experience. The segmentation of experiences in spatial and episodic domains may therefore share neural underpinnings, manifesting in similar behavioral phenomena and cognitive biases. Here, we review evidence for such shared mechanisms, focusing on the key role of boundaries in spatial and episodic memory. We propose that a fundamental event boundary detection mechanism enables navigation in both the spatial and episodic domains, and serves to form cohesive representations that can be used to predict and guide future behavior.**

## Highlights

Both efficient navigation and episodic memory require the detection of crucial junctions separating individual segments of space or experience. In both the spatial and episodic domains, boundaries segregate elements of experience and serve as cues to bind information into cohesive units.

The segmentation of experiences in spatial and nonspatial domains may share neural underpinnings, manifesting in similar behavioral phenomena and cognitive biases.

The interplay between hippocampal and cortical dynamics offers insight into the mechanism by which space and events are segmented.

A crucial question is how different brain regions support coarse versus fine-grained boundary detection. Evidence from patients with localized brain damage or disorders such as dementia provides some insight into this question, but future neuroimaging studies will enable the development of precise mechanistic models.

## Segmentation of Space and Experience

Movement through space is fundamentally tied to movement through time. Our lives are composed of a continuous stream of experience, but we are able to retrieve memories as individual events. Similarly, we can rely on turns and spatial boundaries to segregate routes into segments when navigating in space [1–3]. The ability to retrieve individual episodes from memory crucially relies on a mechanism that efficiently separates events as they occur by imposing boundaries between them, relying on changes in spatial and temporal contexts such as movement between rooms or the time of day [4–6]. Based on the numerous parallels between the neural circuits supporting spatial navigation and episodic memory [7–9], there might also be shared mechanisms that enable the segmentation of physical space during navigation and the segmentation of events in the flow of experience.

In this review we discuss the role of physical and contextual boundaries or discontinuities in the segmentation of spaces and events. We discuss converging evidence from rodent neurophysiology and human neuroimaging to argue that the processes supporting the segmentation of space may provide the scaffold for the segmentation of events in time. By extending the argument from spatial boundaries to episodic context-dependent boundaries, we provide the first formal review of the notion that the segmentation of the continuous temporal flow of experience into discrete events shares key mechanisms with the segmentation of physical space.

We first review the role of physical boundaries and turns in spatial navigation, highlighting their importance in the segmentation of spatial representations. Building on this evidence, we then review parallel findings from naturalistic paradigms, exploring contextual segmentation in audiovisual narratives such as movie clips. Finally, we discuss the key similarities and differences between spatial and nonspatial contextual segmentation, and discuss possible common underlying mechanisms, particularly those related to prediction, planning, and efficient information storage.

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## Spatial Boundaries Shape Environmental and Event Representations

Many of us spend the majority of our time in confined spaces, such as our homes and offices. We are able to navigate between the compartments within them, which requires a reliable representation of the geometry of their layout. Environmental geometry is jointly represented by **place**, **grid**, and **boundary cells** (see Glossary) in the rodent hippocampus and entorhinal cortex [10–12]. Evidence from intracranial recordings suggests a similar neural architecture in humans [13–15]. Specifically, boundary cells in the hippocampal subiculum serve the unique role of firing at the edges of an enclosure, thus establishing the representation of the limits of one's current environment [16–18]. In parallel, entorhinal grid cells provide a cognitive map-like metric by tiling the entire environment with hexagonally symmetric firing fields [19]. This 60° symmetry can, however, be distorted by room structure, such that grid fields in asymmetrical environments are expanded or contracted [20,21]. Recent findings expand the role of such external influences on spatial metrics. Both immediate environmental cues such as local compartment walls [22,23] and salient remote cues visible from the platform [24] were found to shape the framing of the entorhinal grid. Together, these findings suggest that boundaries fundamentally shape global representations of spatial contexts [2].

A key question is how this representation changes when an organism is no longer confined to one space, but moves freely. Movement between spaces necessitates the interaction of landmark-based navigation with path integration, an internally guided and continually updated representation of space [9,25]. How do these mechanisms interact to update neural representations during movement from one space to another? Attempting to answer this question, we review evidence from paradigms exploring (i) movement between confined spaces, and (ii) navigation of routes requiring decisions at junctions along the way.

### Movement between Spatial Contexts

Spatial boundaries modulate the representation of both environmental geometry and the events that occur along the way. When there is a change from one spatial context to another, hippocampal place cells show **remapping**, a phenomenon in which hippocampal cells produce remarkably different firing patterns in different contexts [26–28]. By contrast, when multiple compartments in an environment were visually identical, place and grid cells reinstated their original firing patterns each time a new compartment was entered [29–31]. As rodents moved between compartments, however, hippocampal cells displayed increased firing rates around the doorways [30]. This increase in firing rates at doorways suggests that boundaries separating individual spatial contexts are prioritized and may enable the disambiguation of visually identical contexts supported by the same place and grid cell patterns (Figure 1). Further, the drift in the grid signal that occurred while rats foraged in an open arena was corrected when boundaries were encountered, highlighting their key role in anchoring the grid map [32]. Together, this evidence suggests that boundaries not only signal transitions between contexts [29–31] but also provide structure to the neural basis of the cognitive map [12,32].

Behavioral evidence in humans similarly reflects the importance of spatial boundaries in episodic memory. For example, information is more likely to be forgotten when moving from one room to another [33,34]. This failure to carry over information from one context to another may be the behavioral consequence of remapping, indicating that information is bound to the location where it was acquired and is more difficult to recover as the spatial context changes (Table 1). The recruitment of different neuronal ensembles across boundaries facilitates in accentuating differences between similar contexts, making them orthogonal to one another in memory [35]. A recent study reported that memory for the temporal order of two objects was better when both objects were presented in the same versus an adjacent virtual room,

### Glossary

**Boundary cells:** also known as boundary vector cells, these are cells in the subiculum which code for the boundaries of an environment by responding to its borders.
**Event segmentation/event horizon model:** the theory implemented by this model argues that boundaries are established between events whenever a spike in prediction error (see below) is detected between the current timepoint and the timepoint immediately preceding it, leading to an updating of event models.
**Grid cells:** place-coding cells in the entorhinal cortex (EC) which tile each environment with hexagonally symmetrical firing fields.
**Place cells:** hippocampal cells which respond to particular locations in space. Each place cell responds to a unique location in space. Unlike grid cells, their firing patterns are not symmetrically organized.
**Prediction error:** in the context of event segmentation, it is argued that the brain continuously predicts states immediately following the current one. A mismatch between the current state and the state immediately preceding it is considered to be a prediction error. It is signaled by a spike in activity corresponding to the magnitude to the mismatch which signals the shift in states, and leads to an updating of the event representation.
**Remapping:** when a rodent moves from one compartment to another, the cells firing in the previous environment are no longer active and a new orthogonal ensemble of cells is activated. Remapping also occurs if the initial compartment itself is changed.
**Time cells:** hippocampal cells that fire sequentially, thereby keeping track of the elapsed time, despite the animal remaining in the same spatial location while running on a treadmill.

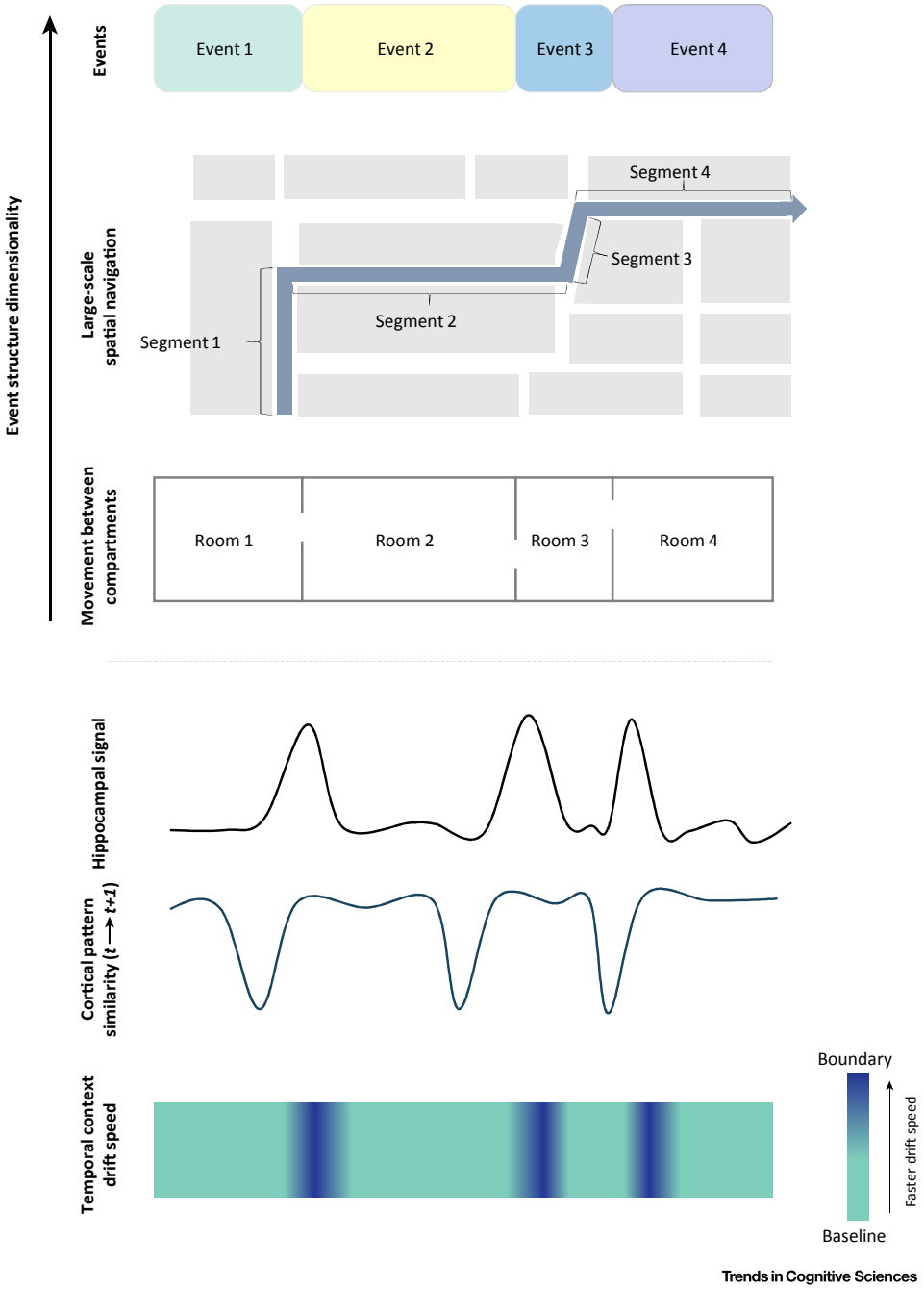


Figure 1. Shared Features of Spatial and Nonspatial Contextual Boundaries. Boundaries between events may be detected on the basis of spatiotemporal context shifts. During navigation, decision-points act as boundaries between road segments. This segmentation is most obvious when turns are made due to a concurrent shift in visual information. Similarly, movement between compartments elicits the remapping between spatial representations. Evidence from event narratives suggests that boundaries produce a peak in hippocampal activity that is preceded by shifts in cortical activity patterns [5,81]. Computational modeling of episodic memory suggests a transient increase in the speed at which contextual representations change over time (temporal context drift) immediately following a spatial boundary [36], repelling events on a mental timeline. Both these phenomena enable the separation of events in space and time, and may stem from the same underlying neural mechanism which requires updating at the boundary to signal a shift in contextual properties.

Table 1. Parallels between Neural and Behavioral Findings Associated with Spatial and Nonspatial Boundaries

| Spatial | Nonspatial |
|---|---|
| Hippocampal remapping when moving between spatial contexts [28,35] | Impaired memory for information across an event boundary [36,78] |
| Route and subroute specific representations in the hippocampus and MTL [40,41] | Event-specific representations in the hippocampus and MTL [5,74] |
| Higher hippocampal and MTL activation associated with decision points in space, such as turns [30,57] | Higher hippocampal and cortical activation at event boundaries [5,69,81] |
| 'Look-ahead' activity at decision points [47]; prospective goal and subgoal representations in the hippocampus [110,111] | Limited empirical evidence in event boundary detection, but theoretical accounts argue that event boundaries are detected due to prediction errors [6,66] |
| Hippocampal–entorhinal map reinstatement by environmental boundaries [29,31,32] | Temporal context reinstatement by event boundaries [79,84] |
| Damage to the hippocampus and MTL results in coarser and more schematic cognitive maps [104,106] | Damage to the hippocampus and MTL results in the detection of coarse, but not fine-grained, boundaries between events [107,108] |
| Cognitive maps constructed and updated by extracting regularities in the environment | Schemas constructed and updated by extracting regularities in experience |

suggesting weaker temporal linking across the boundary separating them [36]. Computational modeling evidence from the same study suggests that this cross-boundary drop in memory was the result of a transient increase in the speed at which the subjective context changes [36] (Figure 1). This transient increase in temporal drift leads adjacent spatial contexts to be repelled on a mental timeline, making them more easily differentiated. Such context-dependent coding, however, is not always disadvantageous. When information on either side of a doorway comprised a standalone unit, boundaries actually resulted in memory improvement by segregating self-contained elements of experience [37]. The type of information being encoded is, therefore, crucial in understanding how spatial boundaries shape memory.

When navigating from one place in the world to another, we rarely find ourselves constrained to enclosed spaces. Instead, we must find our way in our city, which requires (i) the representation of the goal and the optimal route leading to it, and (ii) sequential decisions about whether, and where, to change one's trajectory, both of which may require complex map-like knowledge. Efficient navigation to goals relies on decisions along the way, making segmentation a continuous process. This process begins even when an environment is first encountered, and is recapitulated and refined in subsequent encounters.

## Spatial Boundaries Segment Navigated Routes

The ability to navigate efficiently entails the selection of the optimal route, as well as integration of self-motion and landmark cues to reach the goal [38,39]. The selection of the optimal trajectory requires differentiation between individual routes in an environment, where successive decisions at junction points must be made. Overlap between routes requires reliance on decisions before turns to disambiguate between possible trajectories, resulting in route segmentation. Evidence from rodent neurophysiology suggests that hippocampal neurons exhibit route-specific patterns [40–43]. A subset of neurons showed increased route-specific firing rates only when the rats approached the decision point, reflecting specialized coding for decision points in navigation [41]. In contrast to hippocampal trajectory-specific responses, entorhinal neurons coded similarly for equivalent locations on distinct trajectories [42]. These

findings suggest that the interplay between the hippocampus and entorhinal cortex (EC) supports the extraction of spatial regularities such as turns and boundaries.

Routes in an environment can be represented hierarchically, built up from their component segments. Retrosplenial cortex (RSC) neurons exhibit periodic activation patterns as individual route segments are traversed, while simultaneously maintaining the representation of the entire route [44]. These findings suggest that the RSC extracts route segments and represents them in a hierarchical manner that is embedded within the entire trajectory [45]. Recent work on the perirhinal cortex (PRC) has shown that PRC neurons also exhibit sustained firing patterns throughout entire segments of an environment [46], providing key context-specific input to the hippocampus. Medial temporal lobe (MTL) and related cortices (EC, PRC, RSC) may therefore extract different aspects of route subcomponents which can be incorporated into the unfolding hippocampal representation during navigation. Separable representations of route segments can be flexibly recombined to form novel navigational plans (Figure 2).

Flexible recombination of route segments may underlie the ability to distinguish between competing alternative routes. In support of this hypothesis, hippocampal firing patterns reflected sampling of left and right arms just beyond the turn while the rat is at a decision point on a T-maze [47]. With increased experience on the task, the likelihood of forward sweeps in activity decreased for the unrewarded arm, reflecting the development of expectancy and predictions signals. Such look-ahead activity suggests that decisions are made at junctions along routes by sampling possible future states and relying on this process to plan trajectories [48]. Context-dependent firing is crucial for the formation of predictions shaping future behavior because place cell firing at the same location varied according to whether the decision point was approaching or had already been traversed [49]. Beyond shaping immediate decisions, extended experience with turns along a route shaped patterns of hippocampal theta oscillations [1], which have been proposed as a mechanism bridging the spatial and mnemonic functions of the hippocampus [9,50]. Theta cycles corresponded to individual segments of the environment bounded by turns, reflecting a possible mechanism for cognitive 'chunking' through reliance on stable environmental features. Together, these data suggest that neural representations of temporally extended experiences are fundamentally shaped by spatial boundaries. Given the evidence that boundaries anchor hippocampal firing and constrain oscillations, behavioral correlates of these phenomena should also be observed. Empirical work exploring the effects of boundaries on human memory and cognitive biases provides such evidence (Table 1).

The prominent role of turns as decision points in navigation is reflected in long-term spatial representations in humans. There is a general tendency to compress mentally simulated or imagined routes [51–53], supporting evidence for temporally compressed hippocampal replay in rodents [54,55]. Crucially, routes with more turns, or decision points, tended to be subjectively expanded in time and distance estimates [51,56], indicating that turns act as crucial junctions in memory and mental simulation. Another study reported that different route structures, defined by the location of decision points, may give rise to separable biases in time and distance estimation, with fewer navigation errors being observed at decision points [53].

The importance of decision points during navigation was also reported in fMRI signal properties. In a virtual-reality study where participants learned a route through a museum, objects placed at decision points were associated with higher parahippocampal gyrus activity relative to objects at nondecision points [57,58]. This enhanced activation suggests that representations of objects in locations of particular navigational relevance were prioritized in the brain, reinforced

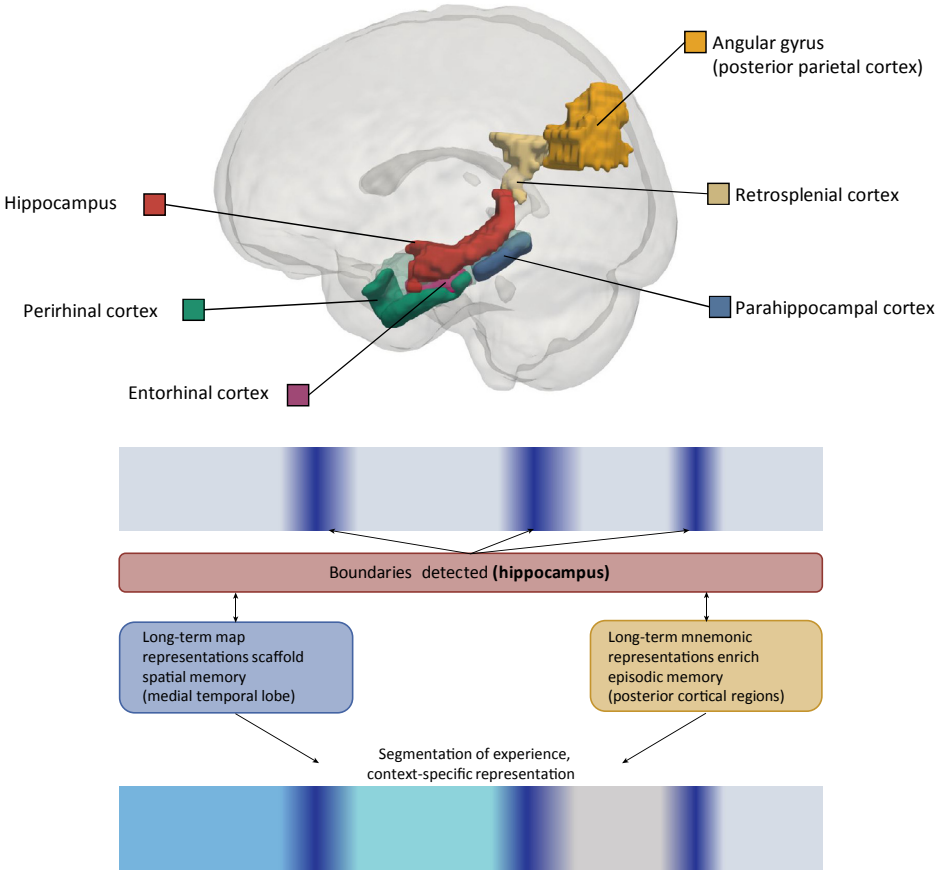


Figure 2. Neural Mechanisms Underlying Context-Specific Representations. The key role of the hippocampus is the coding of ongoing information and the prediction of upcoming states. During the first exposure to a narrative or spatial trajectory, the violation of such a prediction results in a prediction error and the detection of a boundary. The posterior medial cortex, including the retrosplenial cortex and angular gyrus, show a shift in their activity patterns that precede the peak in hippocampal activity, reflecting the multiple timescales at which event structure is encoded. In the spatial domain, activation of the parahippocampal cortex may signal navigationally salient landmarks. This peak in brain activity at the boundary retroactively enhances the representation of events preceding the boundary. Throughout temporally extended sequences of events or spatial contexts, the entorhinal cortex is involved in the extraction of regularities to inform future decision making and provide a schematic scaffold. Through this process, context-specific representations are established and reinforced by pre-existing knowledge structures in the spatial and mnemonic domains (the brain figure was created according to [118–120]).

by the finding that objects immediately preceding decision points were better remembered than those at nondecision points. Further, in a study examining navigation in a real-world environment, posterior hippocampal signal at intersections where participants made navigational decisions increased with goal proximity [59]. By contrast, the EC responded to changes in Euclidean distance, again suggesting that the hippocampus and EC jointly represent possible routes within a large-scale environment. Together, this evidence suggests that contextual discontinuities and their associated stimuli, such as decision points, are preferentially encoded and prioritized in memory and neural representations for navigation. The prioritization of junction points in the environment may enable the extraction of a map-like representation by creating a schematic representation anchored to boundaries (Table 1). Such a schematic map enables the calculation of shortcuts between individual points on the map.

The evidence reviewed so far suggests that humans and rodents rely on physical boundaries or junctions along routes to navigate the physical world and structure future plans. Boundaries between compartments provide cues to shift to new states, shaping unique contextual representations. Similarly, turns along routes signal decision points which produce episode-like segments between each pair of turns. This process is reflected in the manner we give travel instructions – we are likely to provide a sequence of turns guiding an individual from one decision point to the next [60]. This route scaffold can then be enriched by the inclusion of landmarks encountered along the way. Similarly, when we describe events in our lives we often rely on changes in spatiotemporal contexts to separate individual events. Both of these capacities can be supported by the same underlying mechanism, whose function is (i) to learn trajectory- or episode-specific information, and (ii) to learn from commonalities shared across multiple experiences by relying on the ability to extract statistical regularities from our lives and environments [61,62].

## Extraction of Statistical Regularities Enables Cognitive Chunking

To encode both experience-unique information and generalities in the world, a fundamental distinction between hippocampal and cortical coding has been proposed [61,63]. The hippocampus is crucial for rapid episodic memory formation and predictive coding, making this region a promising neural substrate for the detection and extraction of timepoints of particular relevance. By contrast, the cortex gradually acquires the schematic structure of the world. This hippocampal–cortical statistical learning mechanism enables the learning of contingencies between abstract and naturalistic, temporally extended stimuli [62,64].

Hippocampal–cortical processing timescales should also have an impact on the way events are detected within a stream of information and structured in memory. We first review some of the key findings related to the detection of boundaries between events and the structure of event sequences. We will then discuss human neuroimaging of hippocampal–cortical dynamics at boundaries within stimulus sequences and naturalistic paradigms such as narratives and video clips.

### Event Boundary Detection and Context-Specific Representations

Events can often be disambiguated from one another based on their spatial context alone [65]. However, we must frequently rely on conjunctions of changes in spatial and temporal context, and on nonspatial contextual information such as the presence of other people, to establish boundaries between events with overlapping elements. This ability was conceptualized in **event segmentation** theory, which posits that boundaries are established between events whenever there is a sufficient mismatch between the current state and the state immediately preceding it such that a **prediction error** is detected [4,66–68]. A neuroimaging study supporting this view showed that brain activity in a broad network of regions was time-locked to event boundaries, even during passive viewing of videos depicting everyday activities [69,70]. These data provide evidence for the notion that the brain is constantly predicting future states, much as in the spatial domain [47,71], and that events are established when a discontinuity is detected between the predicted and the current state. It is important to note, however, that perceptual differences alone were not sufficient to trigger the establishment of boundaries [70,72], suggesting that the broader episodic context is being predicted.

Event structure is coded in neural patterns at both encoding and retrieval [73], reflected in reinstatement at retrieval [74,75]. Contextual boundaries exert powerful effects on episodic memory similar to those observed in the spatial domain [36]. Both temporal order and associative memory were impaired for adjacent images belonging to different contexts, defined

as stimulus categories, such as faces and objects [76–78]. Interestingly, when freely recalling individual stimuli, participants tended not to cross category boundaries when retrieving strings of items, but nonserial transitions or 'jumps' in retrieval were more likely to be made to items immediately following boundaries [79]. The first item following the contextual category boundary was more likely to be spontaneously retrieved, mirroring the primacy effect in list recall, but retrieval of contiguous items was more likely to be enhanced immediately preceding the boundary. These patterns of behavioral data suggest that boundaries may act as a resetting mechanism, akin to their role in spatial navigation [29,32].

### Hippocampal–Cortical Dynamics at Boundaries

The clustering of stimuli into events is supported by the hippocampus, such that patterns of hippocampal activity were more similar for instances within the same temporal community, or event, relative to across events [80]. The process of segmenting experience into events was reflected in robust peaks in hippocampal activity observed at the offsets of individual video clips [81,82]. The strength of this response was related to subsequent memory for the clips, reflecting information integration and binding. Studies of event boundaries using naturalistic stimuli show reliable correlations in brain activity across subjects, attesting to the robustness of boundaries in guiding the perception of complex material [5,74]. A recent experiment provided compelling evidence that a single extended video narrative can be segmented into several component events on the basis of the change in posterior cortical signal alone [5]. The capacity to integrate information across a gradient of temporal representations may underlie the ability to represent events within a longer narrative, supported by different brain regions operating at different timescales [83] (Figure 2).

The peak in hippocampal activity at the offset of events or at event boundaries [5,81,82] appears to be triggered by pattern shifts in posterior cortical regions such as the posterior cingulate and angular gyrus [5]. When the same narrative was later retrieved, these regions, which were previously strongly coupled with the hippocampus, showed greater degrees of reactivation. This evidence points to a possible cortical hierarchy that enables not only the detection of boundaries but also their integration within a longer narrative and possible enrichment by prior representations (Box 1). The activation of higher-order perceptual and associative cortical regions at boundaries may also reflect brief reinstatement of the just-encoded event to promote more successful encoding [82]. This notion is supported by

#### Box 1. Spatiotemporal Scales and Granularity of Boundaries

Recent neuroimaging evidence and theoretical views suggest that event structure can be represented at multiple timescales [72,74,103]. In parallel, a network of brain regions codes for spatial structure, with different neuronal mechanisms representing different aspects of the environment [13,14]. Aging and damage to specific brain regions result in decreased granularity in both spatial representations and the detection of event boundaries in time. With aging, the ability to form and use spatial cognitive maps is impaired [104], and navigational decision making is increasingly impaired in Alzheimer's disease [105]. At the extreme end of the spectrum, in hippocampal amnesia, spatial representations become schematic and lose fine-grained details [106]. This loss of granularity with hippocampal damage is consistent with evidence that patients with Alzheimer's disease detect coarser, but not fine-grained, boundaries in video clips [107,108]. Findings in both domains point to a loss of granularity owing to an inability to integrate fine-grained details into a global representational scaffold. By contrast, patients with frontal lobe damage are unable to detect coarse-grained boundaries in narratives, but show intact fine-grained boundary detection [109], highlighting the contribution of schematic information to boundary detection, supported by long-timescale regions. In navigation, the prefrontal cortex may support the overall hierarchical structure of subgoals within a route, while the hippocampus codes possible trajectories [110,111]. Even within the hippocampus, a gradient of spatiotemporal representations is observed along the long axis which may enable different levels of granularity in the coding of boundary transitions [112–114]. Future investigations into the nature of boundary coding along the hippocampal anteroposterior axis, and connectivity with cortical regions, will be necessary to test this prediction.

a recent study using scalp electroencephalography which revealed that the content of the just-experienced episode is reinstated at event boundaries [84]. Importantly, the degree of correspondence between neural patterns at encoding and event boundaries was predictive of later memory richness, again suggesting that cortical activity at boundaries is key to memory formation.

The capacity to segment experience into individual events requires the existence of a neural signal that can be shaped by contextual factors. Such a signal would provide a measure of the elapsed time and spatial structure at any given moment. When sufficient time has elapsed, and/or when the spatial surroundings have changed, there is a shift in this signal [85]. A boundary-dependent shift to a new neural representation should therefore make retrieval of information bound to an earlier representation less efficient. Consistent with this hypothesis, walking through doorways and therefore crossing a boundary appears to cause forgetting of events preceding the boundary, and disrupts temporal binding [34,36].

Converging evidence suggests that boundaries between spatial contexts, such as different rooms [36], and more abstract contexts such as different stimulus categories or experimental tasks [78], trigger episodic memory divergence. This idea points to a unified underlying mechanism that enables the segmentation of a temporal signal between physical spaces, as well as between different conceptual contexts (Figure 2). The peaks observed in hippocampal activity at event boundaries [5,82] appear to selectively strengthen the associations among the elements in the chunk of experience immediately preceding it [86]. A possible explanation connecting these findings is that a peak in hippocampal activity and a shift in cortical patterns at the boundary temporarily disrupt the drift of temporal context. We speculate that the baseline rate of context drift is disrupted when population activity at the boundary is implicated in reinstating the preceding information and in binding the individual elements into a cohesive event. Once this binding process is complete, the drift of temporal context would settle back into its previous rate [5,36,81,84] (Figure 1). Together, these data suggest that the hippocampus-mediated detection of boundaries is supported by a broader network of cortical regions which extract generalities in our environments over long timescales.

The evidence reviewed thus far supports the view that contextual boundaries in spatial and nonspatial domains affect memory for how events are encoded and reinstated. Given the substantial overlap observed in boundary-responsive brain regions identified in spatial and nonspatial domains, common mechanisms should underlie these responses. The ability to represent different spatial and temporal scales may depend on the coupling of cortical regions with the hippocampus at boundaries [5]. In both spatial and nonspatial domains, the increased hippocampal activation at boundaries separating spaces or events may tag these junctions and enable the extraction of spatial or event structure. However, a key distinction between spatial and nonspatial contextual boundaries may be reflected in the recruitment of different networks of longer-timescale cortical regions (Box 1). An important avenue for future work will be to delineate the distinction between spatial and nonspatial event boundaries by directly comparing memory and neural signal for items across boundaries separating spaces and abstract contexts. Event segmentation ability has been found to predict memory for events in both younger and older adults [87], and therefore we may predict that this ability should correlate with efficient navigation along extended spatial trajectories (Box 2).

## The Interplay between Boundary Detection and Prediction

A possible underlying purpose of boundary detection in spatial and event memory is the extraction of structure in the world, which enables flexible behavior in similar situations in the

Box 2. Consolidation of Spatial and Nonspatial Boundary Representations

Based on the parallels drawn between transitions between spatial and nonspatial contexts, parallels in the consolidation of learned spatial and nonspatial conceptual information may also be observed. The process of consolidation should be similar in both domains if the hippocampus detects boundaries via rapid episodic learning, while the cortex extracts statistical regularities in the flow of experience [61]. The gradual construction of a spatial cognitive map shares key similarities with the development of schemas (or event models) over the course of one's lifetime. This view is supported by evidence suggesting the existence of a hippocampal–entorhinal nonspatial knowledge structure extracted over the course of learning individual associations [88,115]. This gradual acquisition of a knowledge structure is akin to the development of a cognitive map during navigation [116]. Event knowledge or schemas adaptively improve event memory [87] in the same way that schematic environmental representations guide goal-directed navigation [117]. Long-term representations extracted during learning provide a scaffold for goal-directed behavior in situations with high uncertainty, and enable the flexible modulation of behavior in spatial and nonspatial domains. A key focus for future studies will be to investigate the cortical regions supporting consolidated boundary representations in spatial and nonspatial domains, as well as their interaction with the hippocampus once the consolidated information is activated.

future. Recent evidence suggests that a map-like representation of relationships between abstract stimuli was spontaneously extracted by the hippocampal–entorhinal system [88]. Importantly, such coding was best captured in a model of future state prediction, in line with predictive coding in the spatial domain [47,71]. A recent account provided compelling evidence that, instead of than merely representing the past, the hippocampus plays a foundational role in predicting future states [89]. Under this account, representing the temporal structure of our experience crucially shapes both our memories and predicts future states [90,91]. It has also been argued that the neural architecture supporting map-based spatial navigation can be coopted to support decision-making in other domains [92]. Further, MTL structures and a broader network of ventral visual stream areas coded for navigational affordances, or possible routes one can take in a particular space [93,94]. The hippocampal–posterior cortical code for space therefore represents not only the immediate spatial context one occupies but also represents possible future routes from the current location.

In the domain of event segmentation, a parallel capacity has been expressed in the event segmentation model [68] and was later advanced in the **event horizon model** [6]. These models argue that the ability to detect boundaries relies on prediction error at boundaries. In a manner akin to spatial boundaries, there is a spike in prediction error at boundaries between contexts in narratives, enabling the updating of event representations and a shift to a new representational state [6,66]. Both these accounts share the notion that the hippocampus plays a role in actively predicting future states. Thus, these views suggest that the purpose of both spatial and contextual boundaries is the prediction of future situations in spatial and mnemonic domains. An alternative view argues that the stability of the current context itself may shape the structure of encoded events [95]. According to this theory, evidence is accumulated within each context, producing an episodic memory for all elements sharing the same context [62]. As the context changes (e.g., movement to a different location), the evidence-accumulation process starts anew, and the two adjacent episodic memories are repelled on a mental timeline.

A key difference between the episodic and spatial domains is the relative importance of the boundaries themselves versus the information between each pair of boundaries. In spatial navigation the most meaningful information often relates to the boundaries such as turns rather than to route-specific information between boundaries. Conversely, for episodes the most meaningful information is often what happens between boundaries, rather than the boundaries themselves. However, episodic boundaries may demarcate changes in central elements of an episode (e.g., from searching for groceries to paying for them) and serve as a link between them, much in the same way as a boundary might link adjacent locations on a route. How this

contrast between episodic and spatial boundaries might be differentially supported by the brain is a key avenue for future investigation. Further, the importance of the to-be-remembered information, such as the anticipated reward value, may affect the strength of boundary representations (see Outstanding Questions).

The representation of individual episodes necessarily requires the encoding of experience by temporally extended hippocampal and cortical dynamics, informed by prior experiences, with the aim of efficient goal-directed behavior [96]. Hippocampal 'episode' or **time cells** [97,98] represent a candidate template signal to enable such coding, by providing a signal of elapsed time within each chunk of experience, which can be bound into a cohesive representation of an episode. The firing patterns of these cells during the delay period preceding left- versus right-turn decisions were separable from the first trial onwards, but became increasingly differentiated over several learning trials [99]. A possible interpretation is that this signal is not purely temporal but may also code for the upcoming turn to be made. It is again noteworthy that the period of such elevated firing immediately precedes a decision leading to a shift in spatial context. Importantly, hippocampal theta, that is implicated in goal-directed navigation [100], is crucial for the establishment and maintenance of such intrinsic hippocampal firing fields [101]. These intrinsic dynamics have recently also been reported in nonspatial event sequences [102]. Initial evidence that the properties of theta oscillations can be modulated by environmental boundaries has been provided [1,100], but to what extent this applies to nonspatial contextual boundaries has yet to be established (see Outstanding Questions).

## Concluding Remarks

Integrating the evidence presented in this review, we propose that the mechanism enabling the detection of physical (spatial) boundaries may also support the detection of nonspatial boundaries in stimulus sequences and narratives (Table 1). During spatial navigation, the hippocampus, combining input from other MTL regions, provides a signal that the context is changing. The EC extracts the full structure of a space, while the RSC hierarchically represents subspaces embedded in a trajectory. Whereas boundaries between events in nonspatial narratives are also detected and bound by the hippocampus, more complex narratives may require more extensive integration with prior knowledge. Such integration may depend on schemas that are acquired over the course of a lifetime.

Previously established schemas and event models inform event boundary detection, and this recruits a broader network of cortical regions beyond the MTL, including the medial prefrontal cortex, angular gyrus, and posterior cingulate. By relying on generalities extracted over long timescales, we can optimally adapt our behavior to the current task. Key outstanding questions in this area concern the timescales at which these regularities are extracted and consolidated, how the spatial versus nonspatial aspects of experience drive the detection of boundaries between individual events, and how they are integrated to form a coherent experience. Future investigations directly comparing the effects of spatial and nonspatial boundaries on neural and behavioral measures will provide crucial insight into these questions.

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## Outstanding Questions

What is the precise mechanism by which boundaries enhance memory and bind elements of preboundary information into cohesive events, while disrupting or speeding up the drift of temporal context?

Are boundaries advantageously represented in overlearned environments? When environments are fully consolidated, reliance on boundaries may no longer be necessary because all aspects of the environment are equally useful as navigation cues.

What are the key differences between spatial and nonspatial boundary detection? The evidence discussed here suggests that the hippocampus should play a key role in the segmentation of both domains, but coupled cortical regions may differ for spatial versus nonspatial boundaries.

Are boundaries such as decision points in rewarded trajectories or event sequences represented more distinctively to maximize the likelihood of obtaining the reward?

Are boundaries prioritized for consolidation? Does sleep help the consolidation of boundaries or the information contained between boundaries?

What is the role of the hippocampal–cortical coupling at boundaries? It might reflect the integration of new information with established schemas or the reinstatement of the just-experienced event.

To what extent does event detection depend on visual input? The majority of evidence presented in this review used visual stimuli. While evidence from verbal narratives suggests a highly similar pattern to movie clips, the reliance on visual cues in navigation may impact on the way boundaries are processed in all domains.

Does the granularity of boundaries detected in the neural signal scale along the hippocampal long axis? As the coarseness of representation increases anteriorly, so should the level at which boundaries are detected. The posterior hippocampus may be implicated in

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detection of boundaries based on local differences, whereas the anterior hippocampus may be implicated in detecting differences in global, abstract contexts.

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