

What Is a Cognitive Map? A Critical Review of Its Conceptualization, Neural Basis, and Methods of Construction

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Abstract

Cognitive maps were originally proposed as internal representations of spatial environments that enable flexible navigation and adaptive behaviour beyond rigid stimulus-response associations. Since Tolman's seminal formulation, the concept has expanded dramatically to encompass temporal sequences, conceptual knowledge, social hierarchies, and abstract relational structures. This expansion has generated substantial theoretical and empirical progress, yet it has also produced considerable conceptual ambiguity: what, precisely, qualifies a representation as a cognitive map rather than a simpler associative, schematic, or statistical structure? In this critical narrative review we examine the historical evolution of the cognitive-map construct, its proposed neural substrates (with particular emphasis on the hippocampal-entorhinal system), and the methodological approaches used to identify cognitive maps and to reconstruct their structure from behavioural, computational, and neural data. Here, 'construction' refers to the researcher's methodological reconstruction of putative map-like structure from empirical data, as distinct from the organism's own process of learning such a representation (the latter is addressed separately in Chapter 5). These approaches target relational structure, metric or topological organisation, generalisation, flexible inference, and navigation through representational space, and are contrasted with alternative frameworks that emphasise memory, prediction, or hierarchical coding. Behavioural paradigms, computational models, multivariate neuroimaging analyses, and high-resolution anatomical approaches are compared with respect to their

ability to operationalise map-like representations. Building on this synthesis, we propose a framework that distinguishes the content of a map from the computational and neural mechanisms that encode it, and we discuss how multimodal integration of functional, structural, and microstructural data may refine future investigations. The review concludes by outlining principles for the empirical identification of cognitive maps and by highlighting unresolved tensions between spatial origins and domain-general claims.

Keywords

Cognitive Maps, Spatial Navigation, Hippocampus, Entorhinal Cortex, Relational Representations, Cognitive Spaces, Representational Geometry, Spatial Cognition, Memory, Neuroimaging

1. Introduction: The Problem of Definition

The notion of a cognitive map occupies a peculiar position in contemporary cognitive neuroscience. On the one hand, it is one of the most influential and productive constructs of the past seventy-five years, providing a unifying language for spatial navigation, episodic memory, and, more recently, abstract relational cognition. On the other hand, its very success has rendered the term increasingly elastic. What began as a specific proposal about how organisms represent the spatial layout of environments Tolman [1] has been extended to cover almost any structured internal model that supports flexible behaviour. As a result, the field now faces a definitional problem of the first order: when is it theoretically justified to call a neural or cognitive representation a “cognitive map”, and when does the label become merely metaphorical or even vacuous?

Tolman’s original formulation was explicitly anti-behaviourist. Observing that rats could take novel shortcuts and detours in mazes, he argued that animals construct “something like a field map of the environment” rather than merely chaining stimulus-response associations [1]. This map was conceived as a comprehensive, survey-like representation that could be consulted in novel situations. The subsequent discovery of place cells in the rodent hippocampus [2] and the later identification of grid cells, head-direction cells, and border cells supplied a compelling neural candidate for such a map [3]-[5]. For several decades the cognitive-map hypothesis remained largely tethered to spatial cognition and to the hippocampal-entorhinal circuit.

From the mid-2010s onward, however, a series of high-profile studies began to demonstrate map-like coding in non-spatial domains. Grid-like representations were reported during navigation of conceptual spaces [6], abstract relational structures were shown to be encoded in the hippocampal-entorhinal system [7], and theoretical frameworks were advanced that treated the cognitive map as a general-purpose system for organising knowledge to support flexible behaviour [8] [9]. Parallel work emphasised the continuity between spatial and temporal coding, episodic memory, and predictive processing [10]-[12]. The result has been

a rapid broadening of the construct accompanied by a proliferation of operational definitions that are only partially overlapping.

This expansion raises several interrelated questions that form the core of the present review. First, what are the necessary and sufficient properties that distinguish a cognitive map from other forms of representation: associative networks, schemas, statistical models, or hierarchical feature detectors? Second, to what extent do the neural mechanisms originally characterised in spatial navigation generalise to abstract domains, and when does analogy shade into homology? Third, how can map-like representations be rigorously identified and, in a methodological sense, “constructed” from behavioural, computational, and neuroimaging data? Finally, what role might high-resolution anatomical and microstructural resources play in constraining theories of implementation?

The review is organised as a critical narrative synthesis rather than a systematic meta-analysis. Narrative reviews are particularly suited to conceptual clarification and theoretical integration when the literature is heterogeneous in methods, species, and levels of analysis [13]. We therefore prioritise depth of critical engagement over exhaustive coverage, drawing on both foundational and recent empirical and theoretical contributions. Throughout, we adopt a deliberately sceptical stance toward the uncritical extension of spatial terminology to non-spatial domains, while remaining open to the possibility that domain-general computational principles are indeed implemented by the same neural architecture.

The remainder of this chapter outlines the structure of the review and clarifies its scope. Subsequent chapters examine, in turn, the historical and theoretical evolution of the concept (Chapter 2), candidate neural substrates and their functional properties (Chapter 3), behavioural and computational methods for constructing and identifying cognitive maps (Chapter 4), the extension to non-spatial and abstract domains (Chapter 5), and the prospects for multimodal and microstructural approaches, including those enabled by resources such as BigBrain (Chapter 6). A final chapter synthesises the arguments into a proposed framework and identifies outstanding challenges.

Two preliminary caveats are in order. First, although the review focuses primarily on human and rodent work, we acknowledge that comparative data from other species remain essential for evaluating evolutionary continuity. Second, while we discuss computational models extensively, the emphasis remains on their empirical implications rather than on formal mathematical development. The overarching aim is not to police terminology for its own sake, but to sharpen the theoretical tools required for cumulative scientific progress in understanding how structured knowledge is represented and used by the brain.

2. Methodology

2.1. Approach and Rationale

This paper adopts a critical narrative review methodology. Narrative reviews are particularly well suited to conceptual clarification, theoretical integration, and the

evaluation of heterogeneous literatures that span multiple species, levels of analysis, and methodological traditions [13]. Unlike systematic reviews or meta-analyses, which prioritise exhaustive coverage and quantitative synthesis of narrowly defined empirical questions, a critical narrative approach privileges depth of theoretical engagement, historical contextualisation, and the identification of unresolved tensions. Given that the central aim of the present work is to interrogate the conceptual boundaries, neural underpinnings, and methodological operationalisations of the cognitive-map construct, rather than to estimate effect sizes or catalogue every empirical report, a narrative framework was judged the most appropriate. The review is explicitly critical. It does not treat the expansion of the cognitive-map concept from spatial navigation to abstract relational domains as an unproblematic scientific advance. Instead, it systematically examines the conditions under which the label “cognitive map” is theoretically justified, the extent to which neural and behavioural evidence supports domain-general claims, and the methodological practices that either strengthen or weaken such claims.

2.2. Scope and Inclusion Criteria

The scope of the review encompasses foundational theoretical and empirical contributions to the cognitive-map concept beginning with Tolman [1] and O’Keefe and Nadel [3], electrophysiological, lesion and behavioural studies in rodents that established the hippocampal-entorhinal spatial coding system, human neuroimaging and behavioural studies of spatial and non-spatial relational representations, computational models that formalise map-like representations, recent extensions to conceptual, social, temporal and abstract domains, and multimodal and microstructural approaches including high-resolution MRI and histological resources such as BigBrain. Inclusion was guided by theoretical relevance rather than by a rigid protocol. Priority was given to papers that explicitly engage the cognitive-map construct or its core computational properties, that provide primary empirical or formal evidence bearing on representational geometry, flexible inference or neural implementation, or that offer substantive theoretical critique or alternative frameworks. Purely descriptive anatomical studies, clinical case reports without theoretical linkage, and papers that use “cognitive map” only metaphorically were generally excluded unless they illuminated a specific conceptual or methodological issue.

2.3. Literature Identification and Selection

Relevant literature was identified through iterative searches of major databases including PubMed, Web of Science, Scopus and Google Scholar, using combinations of terms such as “cognitive map”, “cognitive space”, “place cell”, “grid cell”, “hippocampal map”, “relational representation”, “representational geometry”, “successor representation”, together with domain-specific qualifiers. Citation chaining, both forward and backward, from seminal papers was used extensively to capture historical depth and contemporary developments, and the final search across all databases was conducted in April 2026. No formal quality-appraisal checklist was applied,

consistent with the goals of a critical narrative synthesis. Instead, each contribution was evaluated according to the strength of its theoretical linkage to the cognitive-map construct, the rigour of its behavioural or neural measures, the transparency of its analytical choices, and its vulnerability to alternative interpretations.

2.4. Analytical Strategy

The analytical approach proceeded through four interlocking stages. First, a historical-conceptual reconstruction traced the evolution of the construct in order to identify shifts in definitional emphasis and the emergence of ambiguities. Second, candidate defining properties of cognitive maps (relational structure, metric or topological organisation, generalisation, flexible inference, prospective sequencing, and neural implementation by place- or grid-like codes) were extracted from the literature and subjected to critical scrutiny. Third, evidence from spatial and non-spatial domains was compared with respect to behavioural flexibility, representational geometry, and causal dependence on hippocampal-entorhinal circuitry. Fourth, behavioural paradigms, computational formalisms and neural-analytic techniques were evaluated for their capacity to distinguish map-like representations from alternative computational solutions. Throughout, converging evidence across behavioural, computational and neural levels was treated as the strongest warrant for map-like claims, while single-level findings were regarded as suggestive but insufficient.

2.5. Limitations of the Review Methodology

Several limitations should be acknowledged. As a narrative rather than systematic review, the selection of sources inevitably reflects theoretical priorities and may under-represent certain sub-literatures. The rapid growth of work on abstract cognitive spaces means that some very recent findings may not have been fully integrated. The emphasis on conceptual clarification necessarily limits the space devoted to detailed technical exposition of individual experimental protocols or model architectures. These limitations are offset by the gain in theoretical coherence and critical focus that a narrative approach permits.

2.6. Positionality and Theoretical Stance

The review is written from a stance that is sympathetic to the explanatory ambitions of the cognitive-map framework yet sceptical of its unconstrained extension. It assumes that progress in understanding structured neural representations requires both mechanistic detail and conceptual discipline. The proposed working framework offered in the final chapter is presented not as a final taxonomy but as a provisional tool for sharpening future empirical and theoretical work.

3. Historical and Theoretical Evolution of the Cognitive-Map Construct

3.1. Precursors and Tolman's Formulation

The idea that organisms construct internal models of their environments long

predates the formal coining of the term “cognitive map”. Early ethological and Gestalt-inspired work already emphasised relational and configurational properties of perception and action [14] [15]. Yet it was Edward C. Tolman who, in a series of maze experiments with rats, crystallised the notion into a coherent theoretical proposal. In his classic paper, Tolman [1] argued that animals do not merely form chains of stimulus-response associations, as radical behaviourism maintained, but rather acquire “a tentative map... indicating routes and paths and environmental relationships”. Evidence for this claim included latent learning, novel shortcut behaviour, and the ability to navigate around blocked paths: phenomena difficult to accommodate within pure S-R frameworks [16] [17].

Tolman’s formulation was deliberately broad. The map was not restricted to Euclidean metric space; it could include topological relations and even motivational valences. Importantly, Tolman did not claim that the map was necessarily conscious or pictorial; rather, it was a functional construct inferred from flexible behaviour. This functionalist stance later proved both a strength and a source of ambiguity: almost any internal structure that supports flexible inference can be labelled a “map,” thereby risking conceptual dilution.

3.2. The Hippocampal Cognitive Map Hypothesis

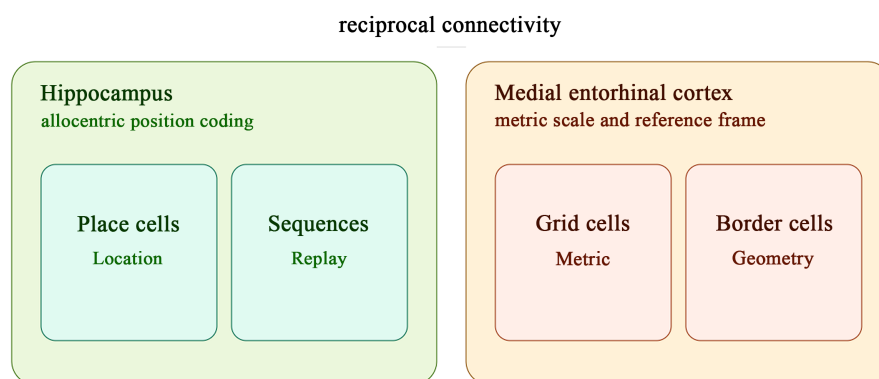
The modern neurobiological instantiation of the cognitive map is inseparable from the work of John O’Keefe and Lynn Nadel [3]. Building on O’Keefe and Dostrovsky’s [2] discovery of place cells (hippocampal pyramidal neurons that fire selectively when an animal occupies a particular location) O’Keefe and Nadel [3] proposed that the hippocampus constructs a Euclidean cognitive map of allocentric space. Their monograph *The Hippocampus as a Cognitive Map* remains a foundational text. They distinguished locale (map-based) from taxon (route- or guidance-based) systems and argued that the hippocampus is specifically required for the former.

Subsequent discoveries reinforced and refined this picture. Head-direction cells [18], grid cells in the medial entorhinal cortex [4], border/boundary cells [19] [20], and speed cells [21] collectively supplied a rich set of spatial primitives.

Figure 1 depicts this canonical circuit schematically, illustrating how place cells in the hippocampus and grid, border, and head-direction cells in the medial entorhinal cortex jointly contribute to allocentric spatial coding through their reciprocal connectivity.

Theoretical models demonstrated how these cell types could jointly support path integration, place-field formation, and flexible navigation [22]–[24]. The hippocampal-entorhinal system thus emerged as the pre-eminent candidate neural substrate for a cognitive map of physical space.

Critically, even within the spatial domain the map is not a simple topographic image. Place fields are influenced by distal landmarks, boundaries, and goal locations; they remap under contextual change; and they exhibit multi-scale organisation along the hippocampal longitudinal axis [25] [26]. These observations already complicate any naïve pictorial reading of the “map” metaphor.



Note. The hippocampus [2] and medial entorhinal cortex [4] [19] form a reciprocally connected circuit that jointly supports allocentric location coding, metric scaffolding, and prospective sequencing [5] [22].

Figure 1. Schematic of the hippocampal-entorhinal circuit implicated in cognitive mapping.

3.3. From Spatial Maps to Relational and Abstract Spaces

From the 1990s onward, a parallel line of research emphasised the hippocampus's role in relational and episodic memory rather than (or in addition to) spatial mapping [27] [28]. Eichenbaum and colleagues argued that the same computational principles that support spatial mapping (binding of elements into relational frameworks) could operate on non-spatial stimuli. This view gained substantial empirical traction with demonstrations that hippocampal neurons can encode temporal sequences, social hierarchies, and abstract task structures [29]–[31].

A decisive conceptual shift occurred in the mid-2010s. Constantinescu *et al.* [6] reported grid-like coding in human entorhinal and medial prefrontal cortex during navigation of a two-dimensional conceptual space defined by the neck and leg length of birds. Garvert *et al.* [7] showed that the hippocampal-entorhinal system represents the abstract relational structure of a learned graph of object associations, even in the absence of explicit spatial demands. These findings, together with theoretical syntheses [8] [9] [32], promoted the idea that the “cognitive map” is fundamentally a system for organising knowledge into relational structures that support generalisation and flexible inference, of which physical space is merely one particularly salient instance.

Bellmund *et al.* [9] advanced the stronger claim that spatial coding mechanisms provide a domain-general format for human cognition (a “cognitive space” in which concepts can be navigated much as locations are navigated in the physical World). Bottini and Doeller [33] further distinguished cognitive maps (allocentric, relational) from image spaces (more viewpoint-dependent), arguing that both operate across reference frames.

3.4. Competing and Complementary Frameworks

The expansion of the cognitive-map construct has not gone unchallenged. Several alternative or complementary frameworks have been proposed:

Memory-centred views [10] [12] maintain that spatial mapping is secondary to the hippocampus's primary role in binding elements of episodic experience.

Predictive-processing and successor-representation accounts [34] [35] reframe place and grid codes as predictive rather than purely spatial.

Hierarchical and multi-scale coding models emphasise that the same circuitry supports nested representations at different levels of abstraction [36].

Schema and systems-consolidation theories [37] [38] focus on the gradual extraction of common structure across episodes, potentially diminishing the need for an explicit “map.”

These perspectives are not necessarily mutually exclusive, yet they differ sharply in what they take to be the core computational problem solved by the system. A critical evaluation must therefore ask whether the term “cognitive map” retains explanatory power once it is stretched to cover all of these functions, or whether more precise terminology is required.

3.5. Persistent Ambiguities and Definitional Criteria

Despite decades of research, no consensus definition of a cognitive map has emerged. Candidate criteria repeatedly invoked in the literature include:

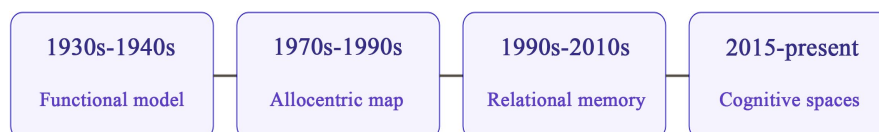
- 1) Relational structure (encoding of pairwise or higher-order relations among elements).
- 2) Metric or topological organisation (distances, angles, or connectivity that can be used for inference).
- 3) Capacity for generalisation and flexible recombination.
- 4) Support for navigation or search through the representational space.
- 5) Neural implementation by place-, grid-, or vector-like codes.

Each criterion is open to interpretation. Relational structure, for example, is also a hallmark of semantic networks and graph-based models that few would label cognitive maps. Metric organisation may be approximate or anisotropic. Flexible behaviour can arise from multiple systems. Neural signatures such as grid-like modulation can appear in tasks whose computational demands are only loosely map-like. Taken together, these criteria suggest a minimal necessary condition: a representation warrants the label ‘cognitive map’ only if it supports generalisation to novel relational inferences that were never directly trained (*i.e.*, zero-shot or few-shot inference over untrained pairwise or higher-order relations among the represented elements).

This condition serves as an explicit disqualifier: a system that reliably reproduces trained stimulus-response or trained pairwise associations, but fails when queried about novel relations implied by, but not directly instantiated in, its training data (for example, failing transitive inference between two items never presented together), does not meet the definition proposed here, however structured or metrically organised its internal representation may otherwise appear.

Figure 2 provides a compact visual summary of this trajectory, tracing the construct's passage from Tolman's rudimentary functional model, through the allo-

centric and relational-memory formulations, to the domain-general cognitive-space accounts that dominate the contemporary literature.



Note. Four successive stages in the conceptual history of the cognitive map, from Tolman's [1] functional internal model to contemporary domain-general accounts of relational cognitive spaces [8] [9]. Colour groups the nodes as a single conceptual lineage and carries no independent variable.

Figure 2. Historical evolution of the cognitive-map construct, 1930s-present.

Table 1 summarises the major historical stages and the corresponding shifts in emphasis.

Table 1. Major stages in the evolution of the cognitive-map concept.

Period	Key Proponents/ Landmark Works	Dominant Emphasis	Primary Evidence Domain	Emerging Tensions
1930s-1940s	[1]	Functional internal model of environment	Rodent maze behaviour	Map vs. S-R debate
1970s-1990s	[3]	Allocentric spatial map	Rodent electrophysiology	Spatial specificity of hippocampus
1990s-2010s	[27]	Relational binding/episodic structure	Human & rodent memory tasks	Space vs. memory primacy
2015-present	[6]-[9]	Domain-general relational/cognitive spaces	Human fMRI, conceptual navigation	Metaphor vs. mechanism; over-extension

The table underscores a progressive abstraction of the construct. Whether this trajectory represents genuine theoretical unification or a progressive loss of precision remains an open and contested question (one that subsequent chapters address by examining neural mechanisms, methodological operationalisations, and the empirical status of non-spatial “maps”).

3.6. Chapter Summary

The cognitive-map concept has travelled a long distance from Tolman's rats to contemporary accounts of abstract knowledge organisation. Each stage has enriched our understanding of how structured representations support flexible behaviour, yet each has also introduced new ambiguities. The central critical task is therefore not merely to chronicle this history, but to extract from it a set of theoretically motivated and empirically testable criteria that can adjudicate when the term “cognitive map” is warranted. The following chapter turns to the neural systems most frequently invoked as the biological realisation of such maps, evaluating the extent to which their properties satisfy (or fall short of) those criteria.

4. Neural Substrates and Functional Properties of Putative Cognitive Maps

4.1. The Hippocampal-Entorhinal Circuit as the Canonical Substrate

The most extensively characterised candidate neural substrate for a cognitive map remains the hippocampal-entorhinal system. In rodents, the discovery of place cells [3] provided the first single-unit evidence that hippocampal principal neurons encode an animal's location within an environment in an allocentric reference frame. Subsequent work revealed that place fields are shaped by distal visual landmarks, geometric boundaries, and path-integration signals, and that they systematically remap when contextual features change [39]–[41]. The longitudinal axis of the hippocampus further exhibits a gradient of spatial scale, with dorsal (septal) place fields typically smaller and more precise than ventral (temporal) fields [25] [26] [42].

Complementing place cells, the medial entorhinal cortex (MEC) contains grid cells whose firing fields form a remarkably regular hexagonal lattice across the explored environment [4]. Grid cells are organised into modules of increasing scale along the dorsoventral axis [43] and are accompanied by head-direction cells [44], border cells [19], and speed cells [21]. Theoretical and experimental work has demonstrated that these cell classes can jointly support path integration, place-field formation via attractor dynamics or oscillatory interference, and vector-based navigation [22]–[24] [45] [46].

In humans, direct homologous evidence is more limited because of the constraints of invasive recording. Nevertheless, intracranial recordings in epilepsy patients have identified place-responsive and grid-like cells in the hippocampus and entorhinal cortex [47]–[50]. Functional magnetic resonance imaging (fMRI) studies have further revealed that the human hippocampal-entorhinal system supports allocentric spatial representations during virtual navigation [51]–[53] and exhibits grid-like hexagonal modulation of blood-oxygen-level-dependent (BOLD) activity when participants navigate open environments [54]–[56].

4.2. Functional Properties Relevant to Map-Like Coding

Several functional properties of the hippocampal-entorhinal system have been taken as evidence of map-like organisation:

4.2.1. Allocentric Reference Frames

Place and grid codes predominantly reflect location relative to the external environment rather than to the animal's body axis [3] [5].

4.2.2. Metric and Topological Structure

Grid cells provide a metric scaffold; place cells and boundary vector cells supply local metric and topological constraints [19] [57].

4.2.3. Remapping and Contextual Modulation

Global and rate remapping allow the same circuitry to represent multiple envi-

ronments or contexts [40] [41].

4.2.4. Multi-Scale Organization

Gradients of field size and grid spacing support representations at multiple spatial resolutions [26] [43].

4.2.5. Predictive and Prospective Coding

Place cells can fire in sequences that sweep ahead of the animal's current location (forward replay and theta sequences), consistent with planning or simulation [58]-[60].

These properties collectively satisfy many of the criteria traditionally associated with a cognitive map. Yet each is open to alternative computational interpretations. Predictive coding and successor-representation models, for example, can generate place- and grid-like patterns without positing an explicit Euclidean map [34] [61]. Likewise, remapping can be viewed as a form of contextual pattern separation rather than the updating of a cartographic representation [62].

4.3. Beyond Purely Spatial Coding: Temporal, Relational, and Abstract Signals

A growing body of evidence indicates that the same circuitry encodes non-spatial variables. Hippocampal neurons in rodents and humans respond to temporal intervals, sequential order, and elapsed time [63]-[66]. Social hierarchy, odour sequences, and abstract task structures can likewise be represented by place-cell-like or grid-like codes [30] [31] [67]. In humans, fMRI studies have demonstrated grid-like coding during conceptual navigation [6], representation of abstract relational graphs [7] [68], and encoding of social and semantic distances [30] [69]. These findings have been interpreted as evidence that the hippocampal-entorhinal system implements a domain-general relational mapping system [8] [9] [32]. Critically, however, the degree of homology between spatial and non-spatial codes remains contested. Grid-like hexagonality in conceptual space, for instance, could arise from generic optimisation principles rather than necessarily reflecting a direct reuse of spatial circuitry [70] [71]. Moreover, many “abstract map” studies rely on multivariate pattern analysis or representational similarity analysis whose sensitivity to fine-grained metric structure is limited [72] [73].

4.4. Extra-Hippocampal Contributions and Distributed Networks

Although the hippocampal-entorhinal system occupies centre stage, cognitive-map functions are unlikely to be confined to it. The retrosplenial cortex, parahippocampal place area, occipital place area, and medial prefrontal cortex all contribute to spatial and scene representation [74]-[76]. Head-direction signals are distributed across a wider network that includes the presubiculum, anterodorsal thalamus, and mammillary bodies [77]. In abstract domains, medial prefrontal and orbitofrontal cortices have been implicated in the representation of task structure and value-based maps [78]-[80].

The existence of these distributed contributions raises the question of whether a cognitive map should be localised to a single circuit or conceived as an emergent property of interacting systems. Network-level accounts emphasise that hippocampal-entorhinal signals are continuously integrated with sensory, mnemonic, and decision-related information [81] [82]. From this perspective, the “map” is less a static internal chart than a dynamic, multi-area constructive process.

4.5. Critical Evaluation: What Counts as Neural Evidence of a Map?

Despite the richness of the data, several critical issues persist. First, the presence of location- or relation-selective firing does not by itself demonstrate that the organism consults a map-like representation; such selectivity could support simpler associative or habit-based strategies. Second, the metric fidelity of neural codes is often imperfect: place fields can be distorted, grid regularity can degrade in complex environments, and human BOLD grid-like signals are typically weak and susceptible to analysis choices [76] [83]. Third, causal evidence that these codes are necessary for map-based behaviour remains incomplete; lesions and optogenetic manipulations disrupt navigation and memory, yet the precise contribution of place versus grid versus other signals is still debated [84]-[86].

Table 2 summarises key cell types and their proposed contributions to map-like function, together with principal limitations.

Table 2. Principal cell types and signals associated with cognitive-map function.

Cell Type/Signal	Primary Location	Proposed Map-Related Function	Key Limitations/Alternative Interpretations	Representative References
Place cells	Hippocampus (CA1, CA3, DG)	Allocentric location coding	Context-dependent remapping; possible sequential/predictive role	[2] [40]
Grid cells	Medial entorhinal cortex	Metric scaffolding/path integration	Degradation in large or complex environments; possible generic optimisation	[4] [43]
Head-direction cells	Presubiculum, ADN, MEC	Orientalional reference frame	Not uniquely hippocampal; present in multiple systems	[18] [44]
Border/boundary cells	MEC, subiculum	Environmental geometry	Primarily local rather than global	[19] [20]
Time/sequence cells	Hippocampus	Temporal structure	May reflect episodic binding rather than temporal mapping	[63] [65]
Grid-like BOLD signals	Human EC, mPFC, etc.	Abstract/conceptual mapping	Indirect; susceptible to analysis pipeline; weak effect sizes	[6] [54]

4.6. Chapter Summary

The hippocampal-entorhinal system, supported by a broader network of cortical and subcortical regions, exhibits a constellation of physiological properties that are consistent with the encoding of structured, relational representations of both

spatial and non-spatial domains. These properties (allocentric coding, multi-scale organisation, contextual remapping, and prospective sequences) supply the strongest available neural evidence for cognitive maps. At the same time, alternative computational accounts, imperfect metric fidelity, and the distributed nature of the circuitry caution against an overly literal or localist interpretation. The critical task for subsequent chapters is therefore to examine how these neural signals can be rigorously linked to behaviour and computation, and how methodological choices influence whether a given representation is classified as map-like.

5. Behavioural and Computational Methods for Constructing and Identifying Cognitive Maps

5.1. Operationalising the Cognitive Map: From Construct to Measure

If a cognitive map is to be more than a useful metaphor, it must be possible to specify the behavioural and computational signatures that warrant the label. This chapter examines the principal methods used to infer, construct, and validate map-like representations. We distinguish three interlocking levels of analysis: 1) behavioural paradigms that probe flexible navigation and inference, 2) computational models that formalise the internal structure required to support such behaviour, and 3) analytical techniques that recover representational geometry from neural data. Throughout, we emphasise that no single method is decisive; the warrant for calling a representation a cognitive map rests on the convergence of multiple, theoretically motivated criteria.

5.2. Behavioural Paradigms

Classic spatial paradigms remain the gold standard for demonstrating map-like competence. In rodents, the Morris water maze [87], T-maze and plus-maze alternation, and open-field foraging with probe trials test the ability to navigate to goals from novel start locations (an ability that is selectively impaired by hippocampal lesions) [88] [89]. Shortcut and detour tasks further probe whether animals can exploit Euclidean or topological knowledge rather than rigid routes [1] [90]. In humans, desktop and immersive virtual-reality environments have enabled analogous tests of survey knowledge, path integration, and landmark-based navigation [51] [53] [91] [92].

Non-spatial analogues have been developed to test whether similar computational principles operate outside physical space. These include:

- Graph-learning and transitive-inference paradigms in which participants or animals learn pairwise relations and are later tested on novel inferences [7] [93] [94].
- Conceptual-space navigation tasks in which stimuli vary continuously along two or more feature dimensions and participants must “navigate” to target locations in that space [6] [95].
- Social hierarchy and value-space tasks that require inference of unobserved

relations [30] [68] [80].

A critical limitation of many behavioural assays is that successful performance can often be achieved by multiple strategies. Route-based, beaconing, or simple associative solutions can mimic map-based behaviour under restricted testing conditions [89] [96]. Careful experimental design (novel start locations, probe trials, and parametric variation of metric versus topological demands) is therefore essential to isolate map-like competence.

5.3. Computational Formalisms

Computational models supply the formal vocabulary needed to specify what a map must compute. Several families of models have been especially influential:

1) Attractor-network and continuous-attractor models of place and grid cells [22] [97] [98]. These demonstrate how recurrent circuitry can maintain a stable spatial representation that is updated by self-motion cues.

2) Oscillatory-interference models that generate grid-like patterns from velocity-modulated oscillators [23] [99].

3) Successor-representation (SR) and predictive-map models [34] [100] [101]. In these accounts, the “map” encodes expected future occupancy rather than a purely geometric layout; place and grid fields emerge as eigenvectors of the successor matrix.

4) Normative models of efficient coding and generalisation [32] [102] that treat the hippocampal-entorhinal system as implementing a relational memory system optimised for compositional inference.

5) Vector-based and boundary-vector cell models that emphasise directed distances to landmarks or boundaries [57] [103].

A task that could adjudicate among these three families is a spatial or conceptual navigation paradigm in which the statistics of experienced trajectories are experimentally decoupled from the geometric layout of the environment (e.g., a fixed two-dimensional arena in which one group of participants/animals is trained with uniform, undirected exploration and another with trajectories that are heavily biased toward a subset of routes or goal locations, while the underlying spatial or conceptual layout is held identical across groups). Continuous-attractor models predict that place/grid-like fields should remain stable and largely independent of trajectory statistics, changing only with path-integration drift or boundary geometry. Oscillatory-interference models predict comparable trajectory-independence but additional sensitivity to running speed and theta-band dynamics not shared by attractor accounts. Successor-representation models uniquely predict that field shape and pattern-similarity structure should skew and compress along the biased trajectories, tracking expected future occupancy rather than Euclidean distance [34]. A behavioural or neural (fMRI grid-score, RSA, or single-unit) outcome showing trajectory-dependent field distortion in the biased group but not the uniform group would favour the successor-representation account; stable, trajectory-invariant fields across both groups would favour continuous-attractor or oscilla-

tory-interference accounts over SR; and differential sensitivity to imposed movement speed versus reward manipulation could further dissociate attractor from oscillatory-interference models.

Each formalism makes distinct empirical predictions. SR models, for example, predict that place fields should distort according to the statistics of future trajectories and that reward should remodel the map [34] [104]. Continuous-attractor models predict path-integration drift and specific patterns of attractor dynamics. The existence of multiple viable formalisms underscores a central methodological point: neural or behavioural data consistent with a “map” are often also consistent with several different computational interpretations.

5.4. Recovering Representational Geometry from Neural Data

Modern neuroimaging and electrophysiological analyses aim to recover the geometry of internal representations directly. Key techniques include:

1) Representational similarity analysis (RSA) and pattern-similarity analyses that test whether the similarity structure of neural activity mirrors the relational structure of the task space [7] [72] [105].

2) Encoding and decoding models that predict neural activity from spatial or abstract coordinates, or recover those coordinates from activity patterns [106] [107].

3) Grid-score and hexagonal-symmetry analyses applied to fMRI time series or virtual-reality trajectories [6] [54] [55].

4) Representational geometry analyses that examine whether neural manifolds preserve metric, topological, or categorical structure [67] [108].

5) Sequence and replay analyses that test whether neural trajectories simulate possible paths through the map [59] [60] [109].

These methods have yielded compelling evidence of structured representations. Nevertheless, they are subject to important caveats. Grid-like signals in fMRI are typically small in effect size and sensitive to preprocessing and multiple-comparison choices [83]. RSA can detect ordinal or categorical structure without guaranteeing metric fidelity. Decoding accuracy does not by itself demonstrate that the decoded variable is used for map-based inference. Consequently, the strongest claims arise when behavioural, computational, and neural evidence converge on the same relational structure.

5.5. Methodological Challenges and Criteria for Identification

Several recurring challenges complicate the identification of cognitive maps.

5.5.1. Strategy Multiplicity

Participants or animals may solve ostensibly map-demanding tasks by non-map strategies.

5.5.2. Confounds of Experience and Statistics

Apparent metric structure may reflect the statistics of training trajectories rather

than an explicit map.

5.5.3. Scale and Generalisation

Evidence of local relational coding does not automatically imply a globally consistent map.

5.5.4. Causal Status

Correlational neural signatures must be supplemented by perturbation or lesion evidence.

5.5.5. Domain Transfer

Demonstrating map-like coding in an abstract space does not prove that the same computational mechanisms are engaged as in physical space.

In light of these difficulties, we propose a provisional set of converging criteria that increase confidence in the presence of a cognitive map (Table 3).

Table 3. Provisional converging criteria for identifying a cognitive map.

Criterion	Behavioural Signature	Computational Signature	Neural Signature	Strength of Evidence When Met
Flexible novel inference/shortcut	Successful detours, shortcuts, transitive inference	Model supports zero-shot generalisation	Neural geometry predicts novel relations	High
Metric or topological consistency	Distance/direction judgements; path integration	Preserved distances or connectivity in model	Recoverable metric/topological manifold	Moderate-High
Multi-scale/hierarchical organisation	Performance across spatial or conceptual scales	Multi-resolution or modular architecture	Graded field sizes or nested representations	Moderate
Prospective/planning sequences	Look-ahead behaviour; mental simulation	Forward sweeps or planning trajectories	Theta sequences, replay of future paths	Moderate-High
Contextual remapping/separation	Context-dependent behaviour	Distinct attractor states or latent variables	Global or rate remapping	Moderate
Causal dependence	Impairment after targeted disruption	Model predicts deficit after component removal	Necessity demonstrated by lesion/optogenetics/TMS	High

No single criterion is necessary or sufficient; rather, the cumulative satisfaction of multiple criteria strengthens the inference that a map-like representation is operative.

5.6. Chapter Summary

Behavioural paradigms, computational formalisms, and neural-analytic techniques together provide a rich toolkit for investigating cognitive maps. Yet each

method is subject to alternative interpretations, and map-like performance or coding can arise from multiple underlying mechanisms. The most robust claims emerge from the triangulation of flexible behaviour, explicit computational models that specify the required internal structure, and neural data that recover corresponding geometry and dynamics. The following chapter examines how these methods have been applied to non-spatial and abstract domains, and evaluates the extent to which the resulting representations satisfy the criteria outlined above.

6. Extension to Non-Spatial and Abstract Domains

6.1. The Domain-General Claim

The most consequential development in the cognitive-map literature over the past decade has been the assertion that the same computational and neural principles that support spatial mapping also organise non-spatial knowledge. According to this view, the hippocampal-entorhinal system, together with interacting cortical regions, constructs “cognitive spaces” in which concepts, social relations, temporal sequences, and abstract task structures can be represented and navigated in a manner analogous to physical space [8] [9] [32]. Physical space is thereby reconceptualised as merely one particularly well-studied instance of a broader class of relational domains.

This domain-general claim rests on three interlocking lines of evidence: 1) behavioural demonstrations of flexible inference in abstract relational structures, 2) neural signatures (especially grid-like and place-like codes) during non-spatial tasks, and 3) computational models showing that the same algorithms can solve both spatial and non-spatial problems. Each line of evidence is substantial; each is also open to critical scrutiny.

6.2. Behavioural Evidence for Abstract Relational Mapping

Classic transitive-inference paradigms already suggested that animals and humans extract ordered relational structures that go beyond pairwise associations [93] [94]. More recent work has expanded the range of abstract spaces. Participants can learn continuous two-dimensional conceptual spaces defined by object features and subsequently navigate or make distance judgements within those spaces [6] [95] [110]. Graph-learning studies show that humans rapidly acquire the relational structure of complex networks and make inferences consistent with an internal map of that structure [7] [111] [112]. Social hierarchies, value spaces, and even narrative structures have likewise been shown to support flexible generalisation consistent with relational mapping [30] [68] [80] [113].

These behavioural results demonstrate that humans (and, in some cases, rodents) can form structured internal models of non-spatial domains. They do not, however, uniquely entail that the underlying representations are metric, Euclidean, or implemented by the same mechanisms used for physical space. Simpler associative, hierarchical, or reinforcement-learning models can often produce comparable behavioural generalisation under the tested conditions [101] [114].

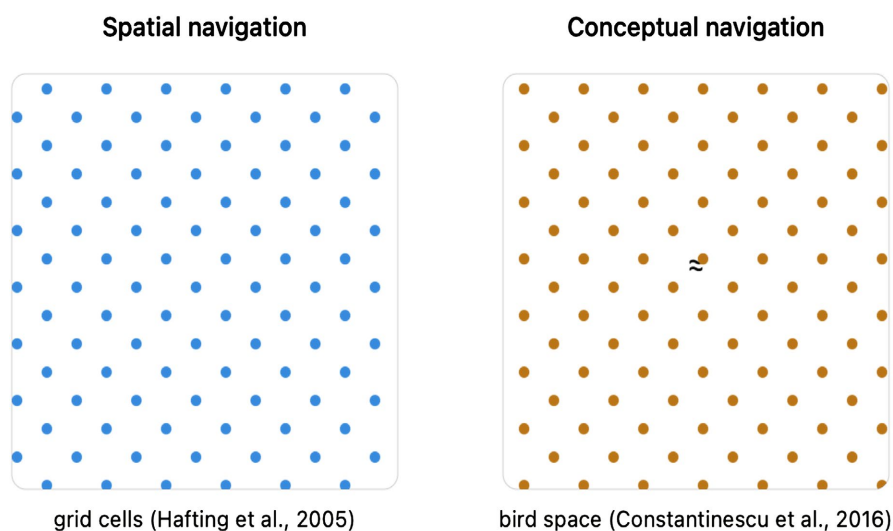
6.3. Neural Signatures in Abstract Domains

The strongest empirical support for domain generality has come from neuroimaging and electrophysiological studies reporting map-like codes outside pure spatial tasks.

6.3.1. Grid-Like Coding in Conceptual Space

Constantinescu *et al.* [6] trained participants to navigate a two-dimensional “bird space” defined by neck and leg length. fMRI revealed hexagonal modulation of activity in entorhinal cortex and medial prefrontal cortex that tracked the direction of movement through this conceptual space (the same signature previously observed during virtual spatial navigation) [54].

Figure 3 juxtaposes the two domains schematically, highlighting how the same hexagonal signature originally reported during physical navigation has also been observed when participants merely navigate a purely conceptual feature space, underscoring the empirical basis of the domain-general claim.



Note. Left: canonical hexagonal firing lattice of entorhinal grid cells during physical navigation [4]. Right: analogous hexagonal fMRI modulation reported during navigation of a two-dimensional conceptual “bird space” defined by neck and leg length [6]. The shared hexagonal geometry across domains is the empirical anchor of the domain-general cognitive-map hypothesis [8], though its interpretive status remains contested [70] [71].

Figure 3. Grid-like hexagonal modulation generalises from physical to conceptual space.

Subsequent studies have reported analogous grid-like signals during navigation of olfactory, auditory, and visual feature spaces [55] [76] [115].

6.3.2. Relational Graph Representations

Garvert *et al.* [7] showed that after participants learned a community-structured graph of object associations, the hippocampal-entorhinal system exhibited a distance-dependent pattern-similarity structure that mirrored the shortest-path distances on the graph, even though no spatial layout had been presented. Related

findings have been reported for social networks and abstract hierarchies [30] [68] [69].

6.3.3. Place-Like and Sequence Coding for Non-Spatial Variables

Rodent and human studies have identified hippocampal neurons that encode position along non-spatial dimensions such as sound frequency, odour morphs, or accumulated evidence [31] [67]. Temporal coding and event-sequence representations further suggest that the same circuitry can map ordered experiences that are not primarily spatial [63] [65] [66].

Collectively these findings demonstrate that hippocampal-entorhinal and related circuits can represent structured non-spatial information. The critical interpretive question is whether the observed codes are genuinely map-like (*i.e.*, metric or topological, supporting flexible navigation) or whether they reflect more generic relational or statistical learning mechanisms that happen to produce similar activity patterns.

6.4. Computational Support and Its Limits

Computational models have played a central role in legitimising the domain-general claim. Successor-representation and related predictive-map models can be applied equally to spatial layouts and abstract state spaces [34] [101] [104]. Whittington *et al.* [32] proposed a Tolman-Eichenbaum machine that learns relational structure across domains using the same architectural principles. Normative accounts argue that grid-like codes emerge from efficient coding of any continuous two-dimensional manifold, spatial or otherwise [46] [70].

While these models demonstrate computational feasibility, they also reveal a potential weakness in the domain-general argument: many of the same signatures can arise from optimisation principles that are not specific to “mapping” in the classical sense. Hexagonal firing patterns, for example, can emerge from computational constraints and optimisation principles, even in the absence of an explicitly spatial representational objective [70] [71]. Thus, the presence of a grid-like neural signature does not by itself prove that the brain is performing spatial-style mapping in an abstract domain.

6.5. Critical Tensions and Alternative Interpretations

Several tensions complicate the strong domain-general interpretation.

First, the metric fidelity of abstract “maps” is often weaker or less well characterised than that of spatial maps. Many studies demonstrate ordinal or categorical structure rather than precise Euclidean metric organisation [73]. Second, the causal necessity of hippocampal-entorhinal map-like codes for abstract inference remains less firmly established than for spatial navigation; prefrontal and other cortical systems may be sufficient for many forms of relational reasoning [68] [78]. Third, the analogy between physical and conceptual navigation can obscure important differences in the underlying statistics and learning demands of the two domains [33]. Fourth, there is a risk of conceptual circularity: once any structured representation

is labelled a “cognitive map,” the claim that cognitive maps support structured representation becomes tautological. A recurring methodological question across the abstract-mapping literature (Sections 6.2-6.4) is whether apparent relational geometry reflects a genuinely learned cognitive map, rather than (a) perceptual or feature-level similarity among stimuli, or (b) the statistical structure of the trajectories participants happened to experience during training. Some paradigms address this directly: Constantinescu *et al.* [6] and Theves *et al.* [95] held low-level visual feature similarity approximately constant across the conceptual space and tested for hexagonal (six-fold) modulation specifically tied to movement direction through the space, a signature not predicted by feature similarity alone. Garvert *et al.* [7] used a graph-learning design in which pattern-similarity effects tracked graph-theoretic shortest-path distance rather than the frequency or recency of co-occurrence during training, partially controlling for trajectory statistics. However, many other studies in this literature (Section 6.2, e.g., social-hierarchy and value-space tasks) do not explicitly dissociate relational geometry from feature similarity or exposure statistics, and instead infer map-like structure from generalisation performance or pattern-similarity effects that remain compatible with simpler associative or exemplar-based accounts [114]. We therefore distinguish claims with direct controls for these alternatives [6] [7] [95] from the larger set of findings [30] [68] [80] that remain inferential: consistent with, but not uniquely diagnostic of, a genuine cognitive map as defined in Section 3.5/8.2.

Table 4 summarises representative studies of non-spatial mapping together with their principal strengths and interpretive limitations.

Table 4. Representative studies of non-spatial and abstract cognitive mapping.

Study	Domain/Task	Key Neural Finding	Behavioural Evidence of Flexibility	Principal Interpretive Caveats
[6]	Conceptual bird space	Grid-like BOLD in EC and mPFC	Distance and direction judgements	Effect size modest; alternative sources of hexagonality
[7]	Abstract object graph	Hippocampal-entorhinal distance coding	Inferential generalisation	Primarily topological; limited metric tests
[30]	Social hierarchy	Hippocampal tracking of social distance	Power and affiliation judgements	Correlational; possible value confounds
[31]	Sound-frequency “space”	Place-like cells in rodent hippocampus	Task performance along frequency continuum	One-dimensional; may reflect sequential rather than map coding
[68]	Social network	Medial temporal and prefrontal relational codes	Novel social inferences	Distributed representation; causal role unclear
[95]	Object-feature space	Hippocampal and cortical distance coding	Generalisation to novel feature combinations	Possible contribution of non-map statistical learning

6.6. Toward a More Differentiated View

A balanced assessment suggests that the hippocampal-entorhinal system and its cor-

tical partners are capable of representing structured information across multiple domains, and that some of the resulting representations exhibit properties historically associated with cognitive maps. At the same time, the evidence does not yet compel the conclusion that a single, unitary mapping mechanism is reused without modification. It remains possible that spatial mapping constitutes a privileged, evolutionarily ancient specialisation, and that non-spatial relational coding recruits partially overlapping but computationally distinct processes [11] [33]. Distinguishing these possibilities will require finer-grained comparison of metric fidelity, causal dependence, and algorithmic implementation across domains (precisely the kind of comparative work that high-resolution, multimodal approaches may facilitate).

6.7. Chapter Summary

The extension of the cognitive-map concept to non-spatial and abstract domains has generated some of the most exciting findings in contemporary cognitive neuroscience. Behavioural flexibility, neural signatures reminiscent of place and grid codes, and domain-general computational models collectively support the idea that relational structure can be represented in a map-like format beyond physical space. Yet important interpretive caution is required: many of the same phenomena are compatible with alternative computational accounts, metric structure is often incompletely characterised, and the precise degree of mechanistic homology remains unsettled. The next chapter considers how advances in high-resolution neuroimaging, microstructural mapping, and resources such as BigBrain may help resolve these outstanding questions by linking representational geometry more tightly to underlying anatomical and cellular organisation.

7. Multimodal and Microstructural Approaches, Including BigBrain Perspectives

7.1. The Need for Multimodal Integration

The preceding chapters have shown that claims about cognitive maps rest on the convergence of behavioural flexibility, computational formalisms, and neural signatures. Yet a persistent gap remains between the functional characterisation of map-like representations and a detailed understanding of their anatomical and microstructural implementation. Functional MRI, even at high field strengths, provides only coarse spatial resolution and indirect metabolic signals. Invasive electrophysiology yields cellular precision but is largely restricted to animal models or limited human clinical contexts. Bridging these levels requires multimodal approaches that link representational geometry to the underlying cellular architecture, connectivity, and molecular organisation of the relevant circuits. This chapter evaluates current progress and future prospects in this direction, with particular attention to the potential contribution of high-resolution histological resources such as BigBrain [116].

7.2. High-Resolution Structural and Functional Imaging

Advances in ultra-high-field (7 T and above) MRI have begun to resolve hippo-

campal subfields and entorhinal subregions in vivo with increasing precision [117]-[119]. These methods have revealed functional differentiation along the hippocampal longitudinal axis and across subfields that aligns with multi-scale spatial coding observed in rodents [26] [42]. Layer-specific fMRI and quantitative MRI techniques further allow the examination of laminar contributions to memory and navigation signals [120] [121]. Diffusion imaging and tractography, especially when constrained by anatomical priors, can delineate the principal pathways linking the hippocampal formation to retrosplenial, prefrontal, and parahippocampal cortices [122] [123].

Despite these advances, *in-vivo* imaging still operates at a mesoscopic scale. Voxel sizes of 0.5 - 1 mm³ remain orders of magnitude larger than individual neurons or even small cortical columns. Consequently, the cellular and laminar origins of map-like BOLD signals (particularly the relative contributions of superficial versus deep entorhinal layers, or of CA3 versus CA1) cannot be resolved directly. This limitation constrains inferences about the precise microcircuitry supporting path integration, relational binding, or abstract mapping.

7.3. Microstructural and Histological Mapping

Post-mortem histological techniques provide the missing cellular resolution. Cytoarchitectonic, myeloarchitectonic, and receptor-architectonic mapping have delineated a complex mosaic of subdivisions within the human hippocampal formation and adjacent cortices that is only partially captured by standard neuroimaging atlases [124]-[126]. Quantitative analyses of neuronal density, dendritic morphology, and synaptic organisation further reveal gradients and discontinuities that may constrain the computational properties of the circuit [127] [128].

The BigBrain dataset [116] represents a landmark resource in this regard. It offers a three-dimensional, histologically reconstructed volume of a complete human brain at 20 µm isotropic resolution, enabling the registration of cellular architecture to MRI space and the examination of laminar and areal organisation at a level of detail previously unattainable in a whole-brain context. Subsequent developments have included multimodal extensions (e.g., integration with receptor densities and connectivity data) and the creation of probabilistic cytoarchitectonic maps that can be projected into individual neuroimaging data [129] [130]. These tools open the possibility of asking whether the microstructural properties of specific hippocampal and entorhinal subregions systematically relate to inter-individual differences in map-like behavioural or neural markers.

7.4. Linking Microstructure to Representational Function

A small but growing literature has begun to exploit these resources. Studies combining quantitative and structural MRI with navigation or memory performance have reported associations between hippocampal structure and spatial or relational abilities [131]-[133]. Cytoarchitectonic probabilistic maps derived from BigBrain and related histological datasets have been used to refine the localisation

of fMRI activations and to test whether functional gradients align with histological boundaries [130] [134] [135]. In principle, such approaches could adjudicate between competing models of cognitive-map implementation (for example, by testing whether grid-like signals preferentially arise from regions with particular laminar or receptor profiles known to support path integration in rodents).

Nevertheless, substantial challenges remain. First, the translation from post-mortem histology to *in-vivo* function is indirect; relationships are typically correlational and subject to the ecological and demographic limitations of the available histological specimens. Second, inter-individual variability in both microstructure and cognitive-map expression is large, necessitating large-scale normative datasets that are only now becoming available. Third, the computational models that formalise cognitive maps are rarely constrained by detailed microstructural parameters, limiting the specificity of the hypotheses that can be tested.

7.5. Prospects for Integrative Frameworks

An integrative research programme linking cognitive maps to microstructure would ideally proceed along several complementary lines:

7.5.1. Individual-Level Multimodal Mapping

Combining ultra-high-field fMRI of spatial and abstract navigation tasks with quantitative MRI and, where possible, histological priors derived from BigBrain-like resources.

7.5.2. Cross-Species Alignment

Leveraging high-resolution rodent and non-human primate data to establish homologous microstructural-functional relationships that can then be tested in humans.

7.5.3. Computational Modelling Constrained by Anatomy

Incorporating laminar connectivity, receptor densities, and cellular composition into network models of place and grid coding (e.g., extensions of continuous-attractor or successor-representation architectures).

7.5.4. Developmental and Ageing Trajectories

Examining how microstructural maturation and age-related decline relate to the emergence and degradation of map-like representations [136] [137].

Table 5 outlines the principal methodological approaches, their current capabilities, and the specific contributions that resources such as BigBrain can make.

7.6. Critical Perspective

While the promise of multimodal and microstructural approaches is considerable, a cautionary note is warranted. There is a risk of assuming that finer anatomical detail will automatically resolve functional controversies. Microstructural differences may constrain, but do not determine, computational function; the same circuit can support multiple algorithms depending on experience, neuromodulation,

and task demands. Moreover, an over-emphasis on histological precision could divert attention from the systems-level and algorithmic questions that remain central to understanding cognitive maps. The most productive path forward is therefore one in which high-resolution anatomical data are used to generate and constrain specific, falsifiable hypotheses about implementation, rather than as an end in themselves.

Table 5. Multimodal approaches to linking cognitive-map function with neural implementation.

Approach	Spatial Resolution	Primary Strengths	Current Limitations	Potential Contribution of BigBrain/Histological Resources
Ultra-high-field fMRI (7 T+)	~0.5 - 1 mm	<i>In-vivo</i> functional mapping of subfields	Indirect signal; limited laminar specificity	Improved anatomical priors for localisation
Quantitative MRI (myelin, iron)	~1 mm	Microstructural proxies <i>in vivo</i>	Indirect; non-specific contrasts	Validation and interpretation of qMRI metrics
Diffusion tractography	~1 - 2 mm	Macroscale connectivity	Crossing fibres; false positives	Anatomically constrained tractography
Cyto-/receptor architectonics	~20 µm (histology)	Cellular and molecular organisation	Post-mortem; limited functional data	Direct source data; probabilistic maps
BigBrain 3-D reconstruction	20 µm isotropic	Whole-brain histological context	Single (or few) specimens; registration challenges	Reference space for multimodal integration
Computational modelling	N/A	Mechanistic hypotheses	Often anatomically under-constrained	Parameterisation by realistic microcircuit data

7.7. Chapter Summary

Linking the functional properties of cognitive maps to their anatomical and microstructural substrates represents a critical frontier. Ultra-high-field imaging, quantitative MRI, and histological resources such as BigBrain provide complementary tools for closing the gap between representational geometry and cellular organisation. Realising this potential will require sustained interdisciplinary effort, careful attention to inter-individual variability, and the development of computational models that incorporate realistic anatomical constraints. The final chapter synthesises the arguments developed throughout the review and proposes a working framework for the identification and investigation of cognitive maps.

8. Synthesis, Proposed Framework, and Outstanding Challenges

8.1. Recapitulation of Core Arguments

This review began with a deceptively simple question: what is a cognitive map? The preceding chapters have shown that the answer is neither simple nor settled. Originally formulated by Tolman [1] as an internal representation of environmental relations that supports flexible navigation, the construct was given a powerful neurobiological foundation by the discovery of place cells and the subsequent

elaboration of the hippocampal-entorhinal spatial coding system [3]-[5]. Over the past decade the concept has been extended to temporal, social, conceptual, and abstract relational domains, accompanied by evidence of grid-like and place-like coding outside physical space [6]-[9].

This expansion has been scientifically generative, yet it has also produced conceptual strain. Many of the neural and behavioural phenomena labelled “map-like” are compatible with alternative computational accounts (predictive coding, successor representations, hierarchical associative learning, or generic manifold optimisation) [34] [70] [71]. Metric fidelity is often imperfect or incompletely tested, causal evidence remains uneven across domains, and the precise degree of mechanistic homology between spatial and non-spatial representations is still unresolved [11] [33]. The central critical conclusion of this review is therefore that the term “cognitive map” retains scientific value only when it is tethered to explicit, testable criteria rather than applied promiscuously to any structured representation.

8.2. A Working Framework for Identifying Cognitive Maps

Drawing on the historical, neural, behavioural, computational, and methodological analyses presented above, we propose a working framework that distinguishes three interrelated but separable components:

8.2.1. Representational Content

The variables and relations encoded (spatial coordinates, temporal order, conceptual features, social rank, etc.).

8.2.2. Computational Architecture

The formal properties of the internal model (metric or topological organisation, multi-scale structure, support for zero-shot inference and path planning, prospective sequencing).

8.2.3. Neural Implementation

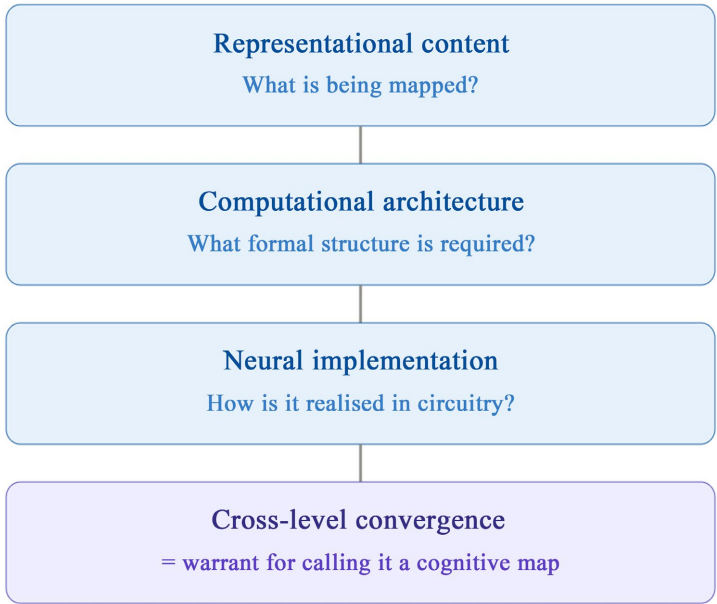
The circuit-level and microstructural mechanisms that realise the architecture (place- and grid-like codes, attractor dynamics, laminar and subfield specialisation, long-range connectivity).

A representation qualifies as a cognitive map, on this account, when there is converging evidence across these three levels that the system maintains a structured internal model whose geometry or topology can be consulted to support flexible, generalisable behaviour beyond the training distribution. Importantly, the framework treats spatial mapping as a privileged but not exclusive case: the same criteria can be applied, with appropriate modifications, to non-spatial domains. It also separates the claim that a map exists from claims about its precise metric form (Euclidean, non-Euclidean, or purely topological) and from claims about the exclusivity of any single neural substrate. This raises an apparent tension: the framework treats neural implementation as one of three separable levels, yet also requires neural evidence of geometry and causal necessity as part of the converging warrant. We resolve this by clarifying the epistemic role of each level.

Representational content and computational architecture are established primarily through behavioural and computational modelling; neural evidence does not independently define a cognitive map but strengthens the inference that a map-like architecture, already motivated behaviourally and computationally, is genuinely instantiated (rather than being an artefact of task design or an alternative non-map strategy). Neural geometry (e.g., grid-like modulation, RSA-derived distance structure) is therefore evidence that constrains which computational architecture is operative, while causal necessity (lesion, inactivation, or stimulation evidence) is evidence that the identified architecture is actually used by the organism rather than merely available. Separating neural implementation as a distinct level thus does not mean neural data are dispensable; it means neural data play a corroborating and constraining role rather than a definitional one.

Consistent with Section 3.5, we take the minimal necessary property of a cognitive map to be support for flexible, untrained relational inference (not mere reproduction of previously reinforced associations). A representational content and architecture that satisfy 8.2.1-8.2.2 but fail this generalisation test (e.g., a lookup table of trained associations with no capacity for novel inference) are disqualified regardless of any structured neural signature identified at the level of 8.2.3.

Figure 4 depicts this framework schematically, showing how converging evidence across the three levels constitutes the warrant for applying the label “cognitive map” to a given representation, rather than to a simpler associative or statistical structure.



Note. A representation is warranted as a cognitive map only when converging evidence is available across all three levels: what is represented (representational content), the formal properties required to support flexible inference (computational architecture), and how these are instantiated in neural circuitry (neural implementation). See **Table 6** for the operational criteria at each level.

Figure 4. Proposed three-level framework for identifying cognitive maps.

Table 6 summarises the framework in operational terms.

Table 6. Proposed working framework for the identification of cognitive maps.

Level	Core Question	Key Evidence Types	Minimum Converging Requirements
Representational content	What is being mapped?	Task design; stimulus dimensions; behavioural reports	Explicitly defined relational structure
Computational architecture	What formal properties does the model possess?	Flexible inference; shortcut/detour behaviour; model comparison	Support for novel generalisation + preserved relational geometry
Neural implementation	How is the model realised in neural circuitry?	Place/grid-like codes; RSA/geometry analyses; causal perturbations	Neural geometry predicts behaviour + necessity demonstrated in at least one domain
Cross-level coherence	Do the levels mutually constrain one another?	Joint behavioural-neural-computational modelling	Predictions derived from one level confirmed at another

This framework is deliberately demanding. It is intended to raise the evidential bar and to discourage both under-claiming (ignoring genuine map-like structure) and over-claiming (labelling any relational code a cognitive map).

8.3. Outstanding Challenges

Several major challenges remain.

First, **metric versus topological organisation**. Many studies demonstrate relational or ordinal structure without establishing metric fidelity. Future work must parametrically test distance and direction coding across both spatial and abstract domains.

Second, **causal specificity**. While lesions and optogenetic manipulations have established the necessity of hippocampal-entorhinal circuitry for spatial mapping, comparable causal evidence for abstract mapping is thinner. Targeted disruption studies in humans (e.g., with transcranial magnetic stimulation or intracranial stimulation) and more refined animal models of conceptual navigation are needed.

Third, **algorithmic diversity**. The field currently entertains multiple viable computational accounts (continuous attractors, oscillatory interference, successor representations, normative efficient-coding models). Progress will require experimental designs that adjudicate among these formalisms rather than merely demonstrating consistency with one of them.

Fourth, **individual differences and plasticity**. Map-like representations vary substantially across individuals and can be reshaped by experience, ageing, and pathology [136] [137]. Linking this variability to microstructural and genetic factors remains a largely open frontier.

Fifth, **integration with complementary systems**. Cognitive maps do not operate in isolation. Interactions with striatal habit systems, prefrontal schema networks, and sensory cortices must be incorporated into any comprehensive account [38] [78] [89].

8.4. Implications for Future Research and Resources Such as BigBrain

The framework outlined above has direct implications for multimodal research programmes. High-resolution histological resources, including BigBrain [116] [129], can contribute by providing anatomically precise priors for the localisation of functional signals, by enabling the testing of hypotheses about laminar and cellular specialisation, and by supporting the development of computationally realistic, anatomically constrained models. The most productive use of such resources will be hypothesis-driven: for example, testing whether inter-individual variation in entorhinal laminar architecture predicts the strength of grid-like coding in conceptual spaces, or whether specific receptor distributions align with the capacity for multi-scale relational binding.

At the same time, anatomical precision alone will not resolve the core conceptual questions. Those questions remain fundamentally computational and functional: what internal structures are required to support flexible behaviour, and how are those structures realised by neural circuits? Microstructural data are most powerful when they constrain answers to these questions.

8.5. Concluding Remarks

The cognitive map has proved to be one of the most resilient and generative ideas in the history of psychology and neuroscience. Its enduring value lies not in any single neural signature or behavioural assay, but in the explanatory ambition it embodies: to understand how organisms construct, maintain, and use structured internal models of the World (spatial and beyond). Realising that ambition requires conceptual clarity, methodological rigour, and a willingness to subject the map metaphor itself to continuous critical scrutiny. By distinguishing representational content, computational architecture, and neural implementation, and by insisting on converging evidence across these levels, the framework proposed here aims to preserve the productive force of the cognitive-map concept while guarding against its dilution. In doing so, it seeks to contribute to a more precise and cumulative science of how the brain organises knowledge for flexible behaviour.

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Author Contributions

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Conflicts of Interest

The author declares no conflicts of interest regarding the publication of this paper.

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