

# An introduction to the Transition Scale-Space model for grid cells

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## Abstract

The hippocampal formation takes a leading part in spatial navigation and episodic memory. Many decades of research revealed prominent neurons with salient responses, in particular place and grid cells. Yet, the individual computational contribution of these neurons within the context of spatial navigation and episodic memory remains debated.

The Transition Scale-Space (TSS) model is a computational and algorithmic model for the representation of sequences and the flow of information within the Hippocampus. It addresses spatial navigation and episodic memories within one conceptual and mathematical framework for sequence processing, and accounts for place as well as grid cells. The first contribute to a memory of spatial locations and temporal events. The latter represent spatial transitions and, thus, information about the relationship between locations, which they relay downstream to place cells. In contrast to other models, hexagonal grid fields and multiple scales of grid modules follow from rigorous mathematical deduction as intrinsic properties of grid cells. Moreover, grid cells of the TSS model operate jointly on afferents from sensory modalities and place cells. In further contrast to other models, each neuron type in the TSS model has a distinct and specialized purpose. The model provides explanations for several other observations that are still unresolved and debated, for instance the wall-angle offset and shearing behaviour of grid fields in square environments or the reason for predominantly inhibitory connectivity within entorhinal cortex. It also yields many testable predictions, such as the fine-structure of connectivity between place and grid cells, and reveals a connection between multiple scales of grid cells and Theta phase precession, a certain temporal dynamic during Theta oscillations. The model generalizes to other transition systems beyond spatial navigation and might also explain the striking similarity between medial and lateral entorhinal cortex.

This paper provides a review of and introduction to the Transition Scale-Space model for grid cells and highlights several testable predictions. It briefly covers other existing models, and identifies similarities and differences. Finally, future research directions that derive from the model are presented.

## 1 Introduction

Spatial navigation is unquestionably an important operation for any mobile creature. It takes a prominent role in behaviour and is an intricate computational problem, yet animals still easily outperform artificial systems in dynamic environments. It is therefore not surprising that neuroscien-

tists, computer scientists, and roboticists are equally eager to unravel its inner workings [9, 63].

The enormous interest in navigation has already led to many scientific results. Seminal behavioural work by Tolman brought him to proclaim “the doctrine of a building up of maps” in both rodents and humans [96]. Research during the subsequent decades found neural evidence in the Hippocampus and adjacent regions that is in support of this idea [65], primarily in form of place [69, 70], head direction [77, 93], and grid cells [38, 91]. Place cells express receptive fields that are spatially localized to predominantly one or only few locations, head direction cells fire when an animal is facing a certain direction, while grid cells show a triangular (or hexagonal) lattice of receptive fields and are organized in modules with a discrete scale-increment. More recent data suggests that place cells also form some multi-scale representation [39, 29], and that the population response of grid cells lives on a toroidal manifold [33].

Despite accumulating data and knowledge regarding a map or map-like representations, many lingering questions remain. This is particularly the case regarding the computations that are performed in the Entorhinal-Hippocampal loop. For instance, it is still debated which function grid cells contribute relative to place cells, why individual grid cell responses are hexonally distributed or why the responses align with a certain small angle relative to the walls of an environment, why grid cell modules show a discretized scale-increment, or which role temporal dynamics such as Theta oscillations and Theta phase precession [44] play during computations.

The Transition Scale-Space (TSS) model for grid cells addresses some of these questions [98, 100]. It was developed with methods from theoretical computer science, graph theory, and information theory, amongst others, and by taking the perspective of Marr’s 2nd level of analysis [57] (“algorithms & data structures”). Thereby, the model is deliberately abstract and the results concerning algorithms and data structures are, in principle, independent from spatial navigation. This also allowed to rigorously and mathematically prove the theoretical results independently of characteristics of the implementation level, in particular non-linear neural and temporal dynamics. As a consequence, the results transfer to other domains that are concerned with storing and retrieving sequential, spatio-temporal, episodic, or relational information. Yet, this approach left the model opaque to those neuroscientists who have only limited experience in the used techniques.

The goal of this article is to present an overview and introduction to TSS that is both, intuitive and accessible, for readers with no or limited background in mathematical meth-



**Figure 1: Ambiguous localization.** Due to multiple responses of grid cells on one scale, a single scale is not sufficient for localization. Summarizing over the responses from multiple scales of grid cells can improve the situation and partially solve this problem.

ods and computer science. To that end, most mathematical details and rigor will be put aside in favour of colloquial explanations. Some details, design justifications, and remarks that go beyond the main goal of the paper are presented in footnotes for interested readers. Several testable predictions will be stated, as well as important future research directions identified for spatial and episodic memory research. Note, however, that this article can not provide an exhaustive survey of existing models for grid and place cells. Still, relevant related work will be mentioned, and some models that are most closely related to TSS briefly discussed to highlight major differences.

## 2 Related Work

This section reviews existing models that are related to or were influential for the TSS model. Similarities and differences between the TSS model and particularly cognate models will be discussed in detail. The discussion will anticipate some of the properties and results of the TSS model, but explain them in depth only in the next section.

A wide variety of models were developed for grid cells. Oscillatory Interference (OI) models are single cell models in which the grid pattern forms due to coincidence detection of velocity controlled oscillators [14, 40], which is supported by some experimental evidence [103]. Another type are Continuous Attractor Network (CAN) models [32, 60, 13], in which the hexagonal pattern appears due to one or multiple bumps of activity that arise from local recurrent interactions within a population of neurons. Evidence for low-dimensional attractor dynamics [108], strong recurrent inhibition [16], as well as the toroidal topology of grid cell population activity [33] are in support of CAN models. Both, OI and CAN models, can accurately path integrate velocity signals, a computation that is widely believed to be at the core of hippocampal processing [80]. Yet, realistic implementations using spiking neural networks of the latter suffer from severe stochastic drift and require stabilization [66]. In other models, grid cells emerge due to afferent connectivity from place cells, for instance due to adaptation dynamics or during the computation of principal components of place cell activity [47, 25], or based on principles from self-organizing maps [61, 49]. Most grid cell models that fit into one of these categories were covered previously in excellent reviews [109, 35, 15].

In many of these models, grid cells are hypothesized to perform path integration or localization. However, a single scale of grid cells is insufficient for localization because the

repeating fields lead to ambiguity, illustrated in Figure 1. A straightforward solution is to summarize over multiple differently scaled grid modules, which can significantly increase the distance between ambiguous representations. Several theoretical works investigated the ideal scaling factor for this approach [58, 90, 102], meaning the scale-increment between consecutive grid modules. While being based on different prior assumptions, for instance local dynamics or integration techniques, all these studies led to theoretically optimal scale-increments in the range of 1.3 – 1.7, which is comparable to biological observations [91]. Others studied how multiple scales of grid cells could emerge in a computational model in which different scales of grid modules were a consequence of a self-organizing process on inputs from multiple scales of other cells [76].

The computational purpose of place cells is less disputed than the purpose of grid cells. Specifically, place cells undeniably participate in episodic memory, spatial processing, and memory consolidation [84, 46]. Using persistent homology on real and artificial data, it was suggested that they provide topological information about an environment [21, 22]. Moreover, they show interesting temporal dynamics in form of pre- and replay, during which previously encountered sequences of place cells fire in order they were traversed in space [83], or in order of future goal-directed trajectories [26, 75], respectively. Experimental evidence suggests that replay in place and grid cells is coordinated [71], hinting towards a co-dependent computation in multiple hippocampal areas. This also emphasizes the nature of the flow of information within the Hippocampus.

The flow of information along the pathways in the Hippocampus forms a loop, also called the trisynaptic circuit [5]. The recently proposed SCAN model focused particularly on the forward projections from place to grid cells in this loop [64]. It is based on a prior CAN model for grid cells [2], but it deviates from the prior work and most other CAN models for grid cells in that it does not rely on integration of velocity signals. Rather, the authors suggest that Hebbian plasticity between spatially modulated non-grid fields and place cells form strong correlates. This means that different sensory inputs lead to activity of different place cells. In turn, plastic connections between place and grid cells then move the activity bump of the grid cell population. Thus, grid cells in the SCAN model effectively track the change of place cell activity, or in other words transitions between place cells. There are significant differences between the SCAN and the TSS model, despite the similarity in what grid cells learn and the fact that also the TSS model does not rely on integration of velocity signals. For instance, grid cells in the SCAN model receive afferents only from place cells, while grid cells in the TSS model jointly operate on both, spatially modulated afferents and place cell activity, to learn and represent how place cells are spatially related relative to sensory inputs. In addition, hexagonal responses of grid cells in the SCAN model are a consequence of at-

tractor dynamics, and multiple scales are assumed to be the result of place cell activity in multiple scales. In contrast, hexagonal responses and multiple scales in the TSS model are explained as inherent to grid cells due to optimal computations, while attractor dynamics are a consequence of implementing these computations in neural circuits.

There exist several further models that attempt to shed a light on joint computations in the Entorhinal-Hippocampal loop. Many of these models focus on navigation and use, for instance landmarks and place codes to find navigational strategies [78]. Others employed linear look-ahead [52] or hierarchical linear-look ahead [30, 31] to find paths between locations by predicting future locations, or showed how grid cell dynamics can be used for navigation around obstacles [27, 28]. Other prior work developed an extensive hippocampal navigation model that was evaluated using robotic systems [19, 20, 41]. This prior work is particularly relevant, given that the authors suggested to study transitions and transition encoding in neural populations to improve navigational capabilities and retrieval. However, this model partially predates the discovery of grid cells and, consequently, no direct link was established between transition coding, place cells, and grid cells. More recent work surveyed the contribution of Hippocampus and in particular time cells and temporal coding to sequencing and navigation, and identified time as an elemental dimension during hippocampal processing [7].

Using a reinforcement learning perspective, others suggested that the Hippocampus forms a predictive map [88]. In an elegant theoretical study, the authors examined successor representations, a dynamics model which represents states in terms of their predictive relationship. They discovered that the eigenvectors of the matrix which represents state-state transitions are periodic and grid-field like. However, the work considered the transition matrix only upon convergence and cannot deal with changes to the transition matrix, which will necessarily occur during exploration. Moreover, reliance on a reinforcement signal poses a serious issue if the model is tasked with spontaneously computing context-modulated trajectories. For instance, it cannot compute trajectories to remote locations that are in conflict with the reward structure of the environment without expensive retraining. The work also does not provide a fundamental explanation for the periodicity, or a constructive method for how grid fields could emerge in a locally distributed, self-organizing, or biologically plausible manner. In contrast, the TSS model provides constructive methods for bottom-up learning. It is also independent of rewards, but can be easily augmented with reward structures or other arbitrary context-modulators.

The idea of a predictive map was recently taken further in form of a cognitive computational model for the hippocampal map, called the Tolman-Eichenbaum Machine (TEM) [107, 106]. The goal of the TEM is to learn to predict the next sensory observation using the current and all previous observations. For spatial navigation, the authors

built their model around a probabilistic formulation for path integration that is conditioned on the action that an agent performs. They note that TEM generalizes to relational information in abstract spaces by conditioning on relational information. Furthermore, they endow their model with hierarchical scales by providing data that was smoothed with differently scaled exponential kernels. The authors provide results that show that their model learns various spatially modulated responses, for instance reminiscent of border cells. They further note that spatial structures are represented using grid-like representations. The TEM is conceptually similar to the previously published TSS model, but the two models have significant differences. In TEM, spatially modulated neurons such as border cells emerge, while they are taken as external input in the TSS model. For the TEM, the authors relate hexagonal grid cell responses to prior results from predictive coding [88] and in particular to a deep learning model [86]. The prior results from the deep learning model need to be treated with caution, however, given that a recent study reported flaws in their interpretation [81]. In the TSS model, hexagonal responses are an intrinsic property of grid cells due to a fundamental neural computation and an optimality result that will be outlined further below [98]. Multiple scales in TEM are extrinsic because the data that it receives is pre-processed into multiple-scales, while in the TSS model, multiple scales are intrinsic to grid cells for optimal acceleration of retrievals [100]. The probabilistic setting of the TEM lends itself to an approximate interpretation in terms of neural firing rates. However, Bayesian inference is not an inductive method for neural dynamics and circuits, meaning it does not directly lead to a biologically plausible blueprint of how spiking neurons could mechanistically perform inference computations [85]. In contrast, the TSS model currently lacks a probabilistic description, but was derived from first principles and with special focus regarding algorithms & data structures. This allowed to define mathematical error functions of individual as well as populations of grid cells in the TSS model, and implement them using biologically plausible neural dynamics [99, 101] (see also Figure 7 below). Another consequence of the (abstract) derivation is that the TSS model generalizes immediately to other domains in which relational information or spatio-temporal sequences are processed, similar to other data structures and algorithms in computer science. In comparison, the TEM was shown to generalize to abstract spaces in some experiments by using carefully designed priors. The broad generalization capabilities that are attested to TEM will, therefore, require further scrutiny. Finally, time takes a prominent role in the TSS model while it is only secondary in the TEM. First, time is an essential part in what and how the TSS model learns to represent, i.e. spatio-temporal and episodic sequences in multiple scales. Second, time played a crucial role during run-time analysis and performance investigations, which motivated the development of multi-scale representations in the first place and which

will be explained in further detail below.

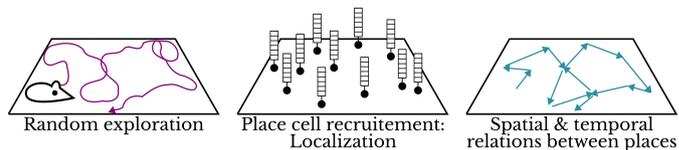
Finally, several models for navigation are based on deep learning [18, 6, 86]. Because some populations of artificial neurons in these models show four- to six-fold symmetric responses, the models were proclaimed to provide insights into real grid cells. However, a recent study investigated these claims and observed that, in these models, the lattice might be a result of tuning parameters and implementation choices, and not of an alleged neural computation [81]. In turn, this study was subsequently refuted by others [87], who noted several issues within the study and pointed out that grid formation of grid cells might follow from the theory of pattern formation [86]. Although it is widely known that many physical and theoretical systems can lead to a variety of observable patterns [97, 17], for instance hexagons, stripes, or spirals, which are commonly referred to as Turing patterns, the patterns themselves rarely give insight into their computational purpose. Interpretations stemming from deep learning models should thus be taken with due care.

### 3 The Transition Scale-Space model

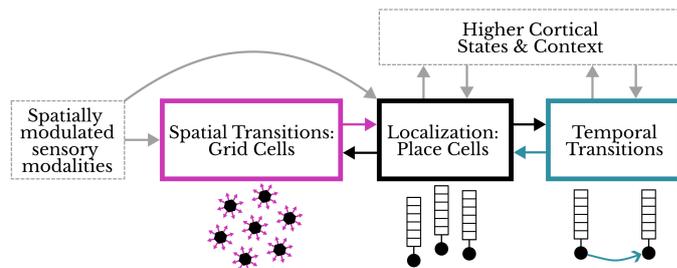
The TSS model is a computational model for the Entorhinal-Hippocampal loop. Its goal is to provide mathematically rigorous and biologically plausible explanations for neural responses within the Hippocampal formation, and in particular for grid cells. It is based on the idea that spatial navigation and episodic memories are two related, in fact congeneric, processes and thus treats both within one conceptual and algorithmic framework. Specifically, both processes are concerned with sequences, which can be motivated from the perspective of navigation.

Spatial navigation consists of at least two distinct but essential parts [42]. One is acquiring sufficient knowledge for localization, another is planning future trajectories relative to and between locations. In fact, one without the other is insufficient. Path integrating travelled distance is meaningless if that distance cannot be related to existing memory of previously visited locations, for instance using some form of chart or map. In turn, accumulating maps and knowledge of locations is without value if there is no information about their connectedness or a retrieval process that makes use of it. Hence, any system that should be used for navigational purposes needs to necessarily address both, illustrated in the context of the TSS model in Figure 2. Learning spatial maps is tantamount to learning maps of temporal events and the temporal order of successive events.

The TSS model consists of three primary neural memories. Each has the purpose of representing particular and distinct information regarding spatio-temporal and episodic sequences. The first memory consists of place cells, which integrate sensory and contextual information for the purpose of localization and storage of temporal events. The second memory is made of temporal transition cells, which exhibit place field characteristics and represent the temporal order in which place cells activated one after another during ex-



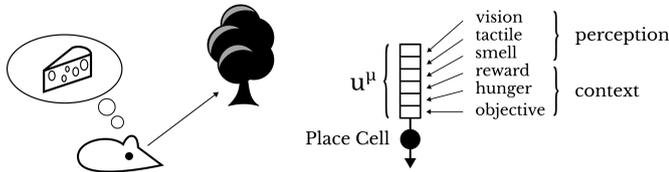
**Figure 2: Navigation.** (left) Random exploration strategy (middle) Place cell recruitment in space. By themselves, place cells in the TSS lack the knowledge of spatial or temporal relationships between each other. They can be interpreted as individual *pins* that are put onto a map, or like location entries in an address book. (right) Information about spatial and temporal transitions between place cells provide the connectivity structure that is required to navigate from one place to another.



**Figure 3: Systems overview of the TSS model.** The TSS model consists of three primary neural memories, which are indicated by solid, coloured lines. Grid cells perform dendritic computation on spatially modulated afferents, whereas place cells are recruited on the basis of spatially and contextually modulated inputs. Temporal transitions are learned directly on top of place cells. Each memory that stores transitions can, in principle, be context-modulated itself. This is illustrated for temporal transitions with gray arrows that point to and away from the memory. The focus of the TSS model is on the flow of information between the three primary memories, as well as internal and recurrent dynamics of each memory. Note that spatially modulated afferents are assumed to be (egocentric) representations which are suitable to identify individual locations, for instance the space of boundary vector or border cells [8, 54, 10].

ploration or mental episodic sequences. The third memory contains grid cells, which, in the TSS model, acquire information about spatial transitions and relations between locations and conveys this information downstream to place cells. A general systems overview of the TSS model is illustrated in Figure 3.

The different neuron types of the TSS model are due to mathematically rigorous results concerning the optimality of representations in the three memories. For instance, the hexagonal arrangement of grid fields in two dimensional, flat environments emerges as a result of optimally compressing data [98], while a discrete scale increment between grid modules follows from optimally accelerating retrievals [100]. Moreover, learning and retrieving sequences in an on-line fashion induces temporal dynamics that are similar to phase precession and pre- and replay of place cell sequences. The following will describe the purpose of each memory as well as their characteristics in more detail, and present intuitive explanations for the mathematical results. Some predictions for biologically plausible implementations or expected behaviour in real neurons will be stated immediately, while



**Figure 4: Place cell representations.** (left) At any point in time, an animal receives sensory information, for instance visual information regarding a distal landmark or the smell of a flower, and has internal states and objectives, for instance a hunger level. (right) The information that is available at one point in time can be represented by a vector  $u^H$ . In the TSS model, place cells are considered to integrate this information, thus *representing* such vectors.

future research directions that are derived from the model will be outlined in the next section.

### 3.1 Place cells integrate sensory and contextual information

Consider an animal that explores a previously unknown environment. Regardless of the specific exploration strategy that is used, such as random exploration or visually driven navigation, it must accumulate sufficient information about the environment that is useful for subsequent and possibly context-modulated operations. For instance, it might need to quickly compute approximate shortest-path trajectories towards a shelter in case of the sudden appearance of a predator, or to a food source if hunger increases. A primary task for a neural navigation system is, thus, to acquire representations of space and trajectories that are suitable for retrieval under biologically plausible dynamics<sup>1</sup>.

A single place cell in the TSS model integrates all afferent information that is available at a certain time  $t$ . Illustrated in Figure 4, the afferent information might consist of all currently available sensory inputs, such as visual perception, tactile information, or smell, in addition to contextual information regarding the animal’s internal state, for instance

<sup>1</sup>The number of neurons in any brain region is finitely countable, and each neuron is subject to stochastic non-linear temporal dynamics. This renders it unlikely that an animal stores a continuous representation of space or traversed trajectories in memory. Take, for instance, a continuous trajectory between two random points  $a$  and  $b$  on some manifold  $\mathbb{R}^N$ , such as the geodesic between the two points. The continuous trajectory can be parametrized as a function  $f : [0, 1] \mapsto \mathbb{R}^N$ , with  $f(0) = a$  and  $f(1) = b$ . It is, in principle, possible to implement this parametrization with spiking neurons based on the relative spike time of two neurons, say  $n_1$  and  $n_2$ . One variant could be to have  $n_1$  encode  $f(0)$ , and  $n_2$  the relative offset from  $f(0)$ . Another could be to have  $n_1$  encode  $f(0)$ , and  $n_2$  encode  $f(1)$ , with their relative spike time being weighted contribution of the endpoints of the trajectory. In either case, this will require infinitely precise relative spike times to accurately decode the true position on the trajectory. Imagine that  $a$  and  $b$  are spatially very far away. Still, a receiving decoder neuron  $d$  that receives spikes from  $n_1$  and  $n_2$  follows its own temporal dynamics. That is, spike times of  $n_1$  and  $n_2$  cannot be arbitrarily far apart *in time*, but need to fit the dynamics of  $d$ . With growing distance between  $a$  and  $b$ , so is the requirement for the decoding precision of spike times between  $n_1$  and  $n_2$ . Assuming biologically plausible noise in the spike times of  $n_1$  and  $n_2$  aggravates the situation even further. It thus appears more likely that an animal stores samples of the environment in conjunction with internal states from which an approximately continuous trajectory can be reconstructed.

its hunger level, reward information regarding the location, or short-term objectives<sup>2</sup>. Thus, the purpose of place cells in the TSS model is to dynamically sample and represent an animal’s state space<sup>3</sup>. Finally, place cells are assumed to reciprocally project back to higher cortical areas<sup>4</sup>, and to be recruited using winner-take-all dynamics during the exploration of an environment<sup>5</sup>.

### 3.2 On temporal transitions and the relational structure of episodic events

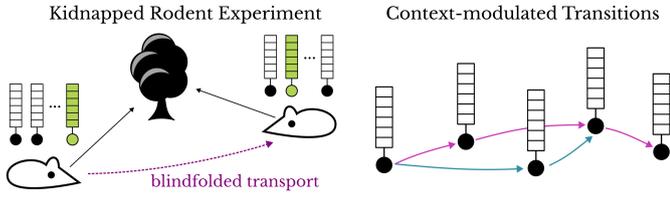
Instead of grouping representations for spatial and temporal events (place cells) with information regarding the order in which events occurred, the TSS model uses a second memory that stores temporal transitions between events. Within this memory, each neuron represents (bundles) multiple

<sup>2</sup>Mathematically, this can be denoted by a vector  $u = (s_1, \dots, s_n, c_1, \dots, c_m)$  which consists of  $n$  sensory items  $s_i, i = 1, \dots, n$ , and  $m$  contextual items  $c_j, j = 1, \dots, m$ . Overall, there might be  $\mu = 1, \dots, N_P$  different vectors  $u^\mu$ , where  $N_P$  depends on the maximal number of patterns that the neural network can handle, or in other words its storage capacity. In the simplest case, a single neuron or place cell could be considered to store one single  $u^\mu$ , but more elaborate methods exist that maximize the storage capacity relative to the number of neurons, for instance Hopfield networks or Willshaw-type neural associative memories [74]. The specific format of each of the  $s_i$  or  $c_i$  are not of concern. Any component of a vector can be approximately represented by a binary string, similar to how data is represented in computers, and with a certain relation to spiking representations. However, binarization might induce quantization issues that need to be addressed. In any case, it suffices to realize that the place cell input is high dimensional, i.e.  $u \in \mathbb{S}^M$  where  $M$  is the dimension of the input manifold, and if place cells perform mapping or localization, that the network dynamics yield a low-dimensional output  $v \in \mathbb{S}^N$  that lives on a  $N$  dimensional data manifold, with  $M \gg N$ , where for two dimensional localization  $N = 2$ .

<sup>3</sup>Note that, in general, the information that is represented by a place cell in the TSS model can be interpreted as both, an individual event in a temporal sequence and as a location in a spatial environment. In the original description for the TSS model [98], the entities storing the vectors  $u^\mu$  were not called place cells, but *symbols*. The terminology comes from the fact that sequences of such vectors can be interpreted as so-called formal languages. In this case, the set of all vectors can be considered to be an *alphabet* for a language, each vector being one symbol. A formal language can then be treated, for instance, with tools from theoretical computer science and graph theory. Other reasons for the change in terminology were to avoid involuntary connotations stemming from the term *place cells*, and to demonstrate that the mathematical and algorithmic results are independent of spatial navigation.

<sup>4</sup>The reciprocal connection of place cells to higher cortical areas is based on ideas from the memory indexing theory for Hippocampus [94, 95].

<sup>5</sup>While it is not a primary focus of the TSS model, it is worthwhile to briefly reason through one approach for the recruitment process of place cells. In a previously unexplored environment, none of the place cells is associated with any of the afferent information that arrives. During exploration, the process randomly picks one of the place cells,  $p$ , and associates it with the afferents at the current time step. If the animal moves away from this specific position, afferent inputs will eventually not match the data represented by  $p$  anymore. Then, the process randomly selects another place cell,  $q$ , and associates it with the new data. This depends on some similarity measure that can compare the information represented by  $p$  and  $q$ , which, in terms of neural activity, could correspond to firing rate changes or relative temporal spike onsets. The process is a simple winner-take-all dynamics and continues until the entire space is explored, or until the number of place cells that are not yet associated is exhausted. This is a standard procedure for instance in self-organizing maps and growing neural gas, and widely used in computational neuroscience [56].

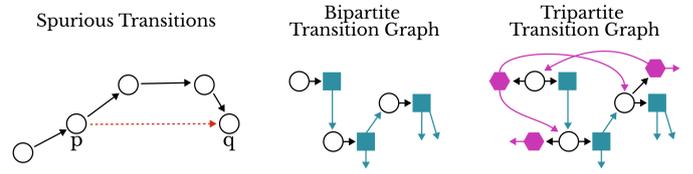


**Figure 5: Reactivation of place cells and contextual modulation of transitions.** (Left) Kidnapped Rodent Experiment. When transporting a blindfolded animal to a known location, the best matching place cell relative to the *new* sensory input activates in the TSS model, indicated by green. The animal thus can localize itself given the prior knowledge of this location. (Right) Context modulation of transitions allows to re-use place cells in different (behavioural) contexts, indicated by different colours for the transitions.

temporal transitions. This provides several benefits which will be discussed below. In particular, it allows to study the limit of the memory’s capacity and solves the problem that contextual information by itself is insufficient for navigational purposes or episodic memory.

Imagine taking the animal from above and, having it blindfolded during transportation, placing it at a distal but already known location as illustrated in Figure 5<sup>6</sup>. Recruiting place cells that represent contextual information during exploration is sufficient for (approximate) localization. That means that once the animal has again access to sensory data, the place cell with the closest match to that sensory data will activate predominantly<sup>7</sup> and, assuming that the purpose of place cells is localization, the animal will know where it is. Yet, this is insufficient to retrospectively activate the elements in the temporal order in which the animal traversed the environment during exploration, which might be important for some tasks. To solve this issue, additional information regarding temporal relations, or more precisely temporal *transitions*, between place cells needs to be stored.

The temporal transition memory of the TSS model has several technical, analytical, and behavioural benefits. The naive approach to represent transitional information is to recurrently connect the place cells in order in which they were recruited or activated during exploration, or by increasing the synaptic strength between successive place cells. However, this suffers from runaway activity and a separate transition memory improves the controllability of sequential retrievals [104, 105]<sup>8</sup>. Two further benefits of a separate tem-



**Figure 6: Spurious transitions and transition graphs.** (Left) Errors during compression (or *bundling*) could produce spurious transitions, indicated by red. They could lead to invalid sequences, and should be avoided. (Middle) The TSS model with place cells and temporal transitions forms a bipartite transition graph. Bipartite graphs in general have two different types of vertices (nodes), indicated by colour and shape. (Right) The TSS model with place cells, temporal, and spatial transitions forms a tripartite transition graph, consisting of three different types of vertices.

poral transition memory are that transitions themselves can be context-modulated during behavioural tasks, illustrated in Figure 5, and that properties of transition memories can be studied in detail.

In fact, one question arises immediately: How many neurons are needed to store temporal transitions in the separate memory? The question follows from the observation that a single transition is only 1 bit of information<sup>9</sup>, and using one neuron to store this bit appears to be wasteful<sup>10</sup>. Therefore, the goal is to compress (or bundle)  $T$  transitions into  $N_T$  neurons in such a way that  $N_T \ll T$ . An important constraint for such a compression is that spurious transitions are avoided. That means that if the animal did not experience a temporal transition from place cell  $p$  to place cell  $q$ , the compression should not lead to the situation in which a retrieval process generates sequences with a transition between  $p$  and  $q$  and, thus, potentially invalid sequences (Figure 6).

It turns out that compressing (or *bundling*) temporal transitions is very limited in the general case [98]. In fact, only those transitions that are “outbound” from one place cell to other place cells can be compressed within one temporal transition neuron. It is not possible to store additional temporal transitions from *other* place cells using that same temporal transition neuron without being at risk of spurious transitions and, thus, violating the constraint that was stated above.

Several observations follow from the theoretical results. The number of temporal transition neurons is at least in the range of the number of place cells. Moreover, temporal tran-

<sup>6</sup>Roboticians call this the “kidnapped robot experiment”.

<sup>7</sup>This behaviour is a certain form of similarity search that is well studied in both, computational models for associative memories and real systems such as the Hippocampus [82, 89, 67, 79]. Essentially, the search is a pattern completion process for a partial or disrupted input pattern  $\tilde{u}^\mu$  which is similar enough but not equal to the original pattern  $u^\mu$ . Another variant to achieve this behaviour is a simple winner-take-all dynamics based on nearest neighbour search.

<sup>8</sup>Technically, the population of place cells of the TSS model can be implemented as an attractor network with multiple attractors, where each location corresponds to one attractor that depends on the input to the network. By adding recurrent connectivity that stores transitional information, the population of place cells exhibits, in addition to its main functional purpose, a structure similar to synfire chains. Prior studies showed that

controlling the speed or retrieval of sequences in synfire chains and associative memories is non-trivial [104, 105]. In particular, background noise or afferent inputs can induce an autonomous mode in attractor networks where one attractor is selected randomly or in which the system even starts to unvoluntarily move through the entire state space. The separate memory of the TSS that stores temporal transitions provides improved control over such behaviour.

<sup>9</sup>“Is there a transition from place cell  $p$  to place cell  $q$ ?” can be answered with a yes/no response. From the perspective of information theory, this is effectively 1 bit of information.

<sup>10</sup>The capacity of Hopfield networks and Willshaw-type neural associative memories has been studied extensively [72, 73, 4]. Given sparse input patterns, the asymptotical capacity that can be achieved is on the order of 0.72 bit *per synapse*. Recent work on Modern Hopfield networks attempts to push this limit even further [48].

sition neurons will exhibit place fields. That is, a transition neuron will activate in conjunction with its corresponding place cell for which it stores transitions. From a graph theory point of view, the system forms a directed bi-partite graph, with one type of vertices (nodes) in this graph being place cells, and the other type representing the temporal transitions to other place cells<sup>11</sup>, illustrated in Figure 6.

### 3.3 Spatial transitions and the hexagonal distribution of squishy fields

The TSS model uses a third memory to store spatial transitions. The reason is that temporal and spatial transitions differ significantly in their structure. Temporal transitions, which were considered in the previous section, underlies the assumption that arbitrary transitions between *any* place cells  $p$  and  $q$  are feasible. This is relevant, for instance, for systems that are tasked predominantly with episodic information. The physical space in which an animal navigates is, however, quite different. Primarily, immediate transitions between arbitrary remote locations are physically not feasible without crossing through other locations. This has substantial consequences for spatial transitions and, in particular, how to optimally bundle them<sup>12</sup>. Effectively, the difference between temporal and spatial transitions gives rise to spatial transition neurons: grid cells.

Grid cells in the TSS model are subject to the same considerations as temporal transition neurons. Specifically, each grid cell is supposed to bundle as many spatial transitions as possible to maximize the memory capacity and to minimize the number of neurons required in the third memory. Similar to temporal transition neurons, a grid cell can only represent disjoint transitions to avoid spurious transitions, meaning it can not represent any transition that starts in a region of one of the other transitions that this grid cell represents. To understand the implications of this for bundling spatial transitions, it is first necessary to characterise the properties of spatial transitions.

<sup>11</sup>The bipartite graph has a natural connection to factor graphs and probabilistic models, with the main difference being the directedness of the graph. It thus appears straightforward to augment the graph with notions of probabilities and uncertainty and run, for instance, the sum-product algorithm to evaluate local marginal distributions.

<sup>12</sup>In the lingo of theoretical computer science and formal language theory, place cells can be interpreted as letters or symbols of an alphabet. More precisely,  $p_i \in \Sigma$ , where  $\Sigma$  denotes the alphabet and  $p_i$  the  $i$ -th place cell or letter. A word over the alphabet is then any finite sequence of letters from the alphabet, for instance  $p_7 p_3 p_1$ .  $\Sigma^*$  denotes the set of *all* words over the alphabet, where  $*$  is the Kleene star operator. Then, a formal language  $L$  over the alphabet  $\Sigma$  is a subset of  $\Sigma^*$ . In the case of temporal transitions, the assumption is that the language that is formed by interpreting place cells as letters is  $L_t = \Sigma^*$ , meaning that any two place cells  $p_i$  and  $p_j$  might be temporally adjacent. This is in contrast to the language that is induced by spatial transitions. In this case, the language is *endowed* with an additional spatial distance metric  $\mathcal{D}$ , and the “spatial language”  $L_s$  consists only of words in which  $p_i$  and  $p_j$  are spatial neighbours, meaning within a certain distance  $\mathcal{D}(p_i, p_j) \leq \theta$ . If  $p_i$  and  $p_k$  are not spatial neighbours, i.e.  $\mathcal{D}(p_i, p_k) > \theta$ , they cannot be adjacent letters in words within the “spatial language”  $L_s$ .

Spatial transitions are captured by on-center and off-surround dynamics in the TSS model [98]<sup>13</sup>. Intuitively, a spatial transition begins at a certain perceivable location, called its *domain*, and can lead to any location in the neighbourhood surrounding this location, called its *image* (see Figure 7). Furthermore, a spatial transition is not defined for locations beyond the surround neighborhood, given that such transitions are not physically feasible<sup>14</sup>. A single spatial transition is thus only defined for a small portion of the space, identified for instance by sensory modalities, and not the global space in which an animal navigates<sup>15</sup>.

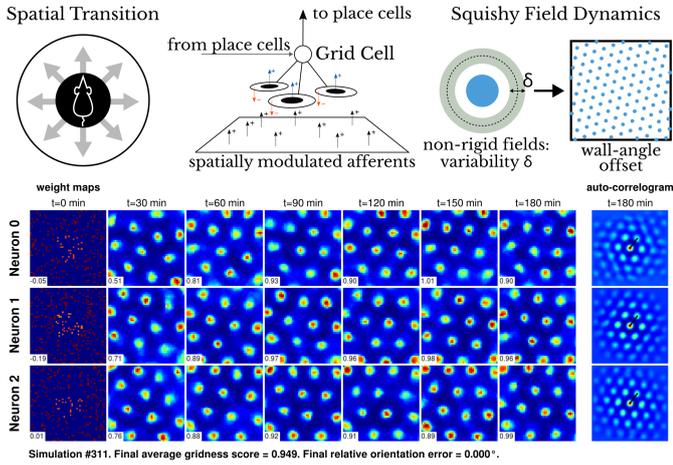
Each grid cell of the TSS model maximizes the number of spatial transitions that it can represent. Due to the structure of spatial transitions, this means that each grid cell attempts to densely pack as many on-center and off-surround receptive fields on afferent sensory information<sup>16</sup>. In the TSS model, the packing of fields is considered to be part of the dendritic computation of each grid cell (see illustration in Figure 7). The densest packing of such fields in an open environment, and thus the optimal bundling of spatial transitions, results in a hexagonal lattice [98]. In the theoretical limit in which any grid cell can represent an arbitrary number of spatial transitions, only three grid cells are required in total. While this is biologically implausible, the key insight is that there

<sup>13</sup>On-center and off-surround dynamics for spatial transitions are, in fact, a result of optimal bundling [98]. This means that these dynamics are not preordained, but a consequence of the computations that grid cells in the TSS model perform. Details about this construction are omitted from this paper for the sake of clarity and to avoid the introduction of further technical jargon and complexity.

<sup>14</sup>Note that the TSS model explicitly assumes that individual locations can be inferred from spatially modulated sensory afferents. This means that the definition of a spatial transition requires that locations can be identified and disambiguated from neighbouring locations, and that this is the functional part of the on-center fields of grid cells in the model. A prior theoretical model for place cells demonstrated that information regarding an animal’s distance towards boundaries is sufficient for the generation of place cell responses [8], and subsequent studies found evidence for the existence of such data in the Hippocampus [54, 10]. It is therefore safe to assume that there exists afferent sensory information which is sufficiently rich to allow this kind of discrimination, and that each perceivable and distinguishable location is characterized by a certain spatially modulated *signature*. Note that, hereby, locations with the same or almost identical sensory stimuli are expected to activate the same grid cell, as seen in the fragmentation of grid maps in hair-pin mazes [23], and that distortions that originate in sensory afferents are expected to translate to distortions in grid fields, similar to grid field deformations due to environmental geometry [51, 50].

<sup>15</sup>The definition of spatial transitions in the TSS model is similar to the definition of a chart of an atlas in differential geometry. In fact, the TSS model can compute shortest path trajectories precisely because of this relation on arbitrary Riemannian manifolds [100]. Moreover, the transitions of the TSS have a certain conspicuous relationship to mathematical (total) differential operators, meaning that they represent the change along all directions. However, further work will be required to identify the properties of such an operator and to establish a full mathematical picture.

<sup>16</sup>The mathematical proof in the original work derived the optimality result using the Petersen-Middleton theorem for sampling from a higher dimensional band-limited signal, and a subsequent reduction to a graph colouring problem [98]. Sphere packing provides, however, a more intuitive understanding of the proposed computation that is performed in the dendritic tree of a grid cell. There is a direct correspondence between the proof, in particular the sampling theorem, and sphere packing.



**Figure 7: Spatial Transition, Dendritic Computation, Squishy Field Dynamics, Biologically Plausible Simulations.** (top left) A spatial transition is defined in the TSS model for a certain location that is identifiable in sensory space, and leads to the entire neighbourhood of similar sensory representations. (top middle) A grid cell performs identification of spatial transitions in form of on-center and off-surround receptive fields and dense packing of the receptive fields as part of its dendritic computation. It conveys the information about a spatial transition downstream to place cells. (top right) Dense packing of receptive fields that are subject to slight variability (*squishy fields*) in rectangular environments consistently yields a wall-angle offset that is comparable to grid field distributions of real rodents. (bottom) Simulations of neural dendritic weights that follow biologically plausible plasticity dynamics during random exploration of a square environment. The results show stable dendritic weights over the duration of the simulation, and wall-angle offsets and slight shearing that are similar to observations from real grid cells [92]. The first seven columns show the evolution of the plastic dendritic weight maps at different times of the simulation, with random initialization at  $t = 0$ , the last column depicts the auto-correlogram for each weight map. The simulated animal randomly explored the environment during the entire simulation following movement statistics that were based on rodent data. This particular simulation had a final gridness score of 0.949. Figure partially reproduced from [99].

is a comparably small, finite number of grid cells required to cover large, behaviourally relevant spaces [98].

In biologically plausible and real networks, individual grid fields are unlikely to be rigid, but show some variability. That means that while a grid field generally is expected to follow the on-center and off-surround dynamics that are described above, the dynamics might vary slightly from field to field or express other imperfections. Moreover, the dynamics depend on the sensory afferents on which the center-surround fields are packed on, which might bring further imperfections. Overall, this potentially leads to a *squishiness* of grid fields. The behaviour of such *squishy fields* can be simulated to study expected distributions of real grid fields in different environments [98]. In fact, it turns out that simulating the dense packing of squishy fields consistently leads to wall-angle offsets in the range of observations from real grid cells [92]. This wall-angle offset is commonly assumed to be a requirement for computations that *rely* on symmetry breaking during (or in addition to) an anchoring or localization process. In contrast, the TSS model suggests that they are

simply the *by-product* of optimal dendritic computations<sup>17</sup> that densely pack receptive fields<sup>18</sup>, and derive from the geometric structure of the environments that rodents are exposed to during trials. The wall angle offset also appears in simulations of neurons and their dendritic weights with biologically plausible dynamics (see bottom row of Figure 7).

In the TSS model, a population of grid cells needs to be maximally competitive [98]. The reason is similar to the argument regarding spurious transitions, but also follows from the minimization of required grid cells. Two grid cells that represent spatial transitions which start from the same location are immediately in violation of the constraint to reduce the number of grid cells. At the same time, if the cells encode transitions starting from similar but distinguishable locations, co-activation could lead to spurious transitions. Therefore, the population dynamics need to exhibit winner-take-all characteristics to avoid co-activation of multiple cells, for instance with strong recurrent inhibition between grid cells<sup>19</sup>. However, a biologically plausible implementation is

<sup>17</sup>The proposed biological nature of the dendritic computations can be understood as follows. Assume a certain number of presynaptic spatially modulated neurons [8, 54, 10]. Inspired by relative spike latencies of retinal neurons [36], further assume that the spike time of each of these neurons is relative to the stimulus onset and its preferred stimulus. This means that a neuron is expected to spike almost immediately given its preferred stimulus, and systematically later depending on the match between the actual and preferred stimulus. At a certain time  $t$ , a grid cell will then need to synapse (or correlate) with the “early” presynaptic inputs to establish the start of the transition. In addition, this grid cell has to decorrelate from “late” spikes, because they carry information about similar but neighbouring locations and, thus, the target region of the transition. The correlation/decorrelation process can be well described as local dynamics using asymmetric spike-timing dependent plasticity kernels. Given suitable presynaptic input, this leads to dense packing of circular fields. That means that the distribution of grid fields should derive from presynaptic activity. In other words, grid fields in open rectangular spaces are likely hexagonal because sensory stimuli are similar to each other, and the distribution of grid fields should change in accordance with changes in presynaptic inputs in more complex environments [51, 50]. More details, discussion, and simulation results can be found in the prior work [101, 98, 99].

<sup>18</sup>Simulating dense packing of squishy fields reveals that the hexagonal packing in two dimensions is a minimum-energy configuration that can be easily attained. In higher dimensions, the minimum-energy configuration should again follow results from sphere packing theorems. However, there are several other low-energy configurations which appear to be local minima and which are more easily discovered by the system dynamics. These low-energy configurations do not show a “nice” hexagonal distribution of the fields. Rather, the fields are irregular and look “all over the place”. This might explain the distribution of grid fields in animals that traverse three dimensions [37, 34], and have implications for future research.

<sup>19</sup>Evidence from rodents suggests that recurrent connectivity within Medial Entorhinal Cortex (MEC) is predominantly inhibitory [16]. However, Parvabulmin-expressing interneurons (PV neurons), which are known to provide strong and rapid recurrent inhibition, lack a clear spatial tuning similar to grid or place cells [12]. This poses a problem for CAN models of grid cells which rely on specifically tuned inhibition that depends on the phase of a grid cell. In contrast, the TSS model requires only that winner-take-all dynamics are fast, but the inhibition can be diffusive. That means that after one grid cell spikes, all grid cells should be silenced. An implementation of a small network of TSS grid cells, in which the model neurons follow biologically plausible dynamics but directly and instantaneously inhibit each other, shows clear hexagonal pattern formation [99], illustrated in Figure 7. A more elaborate implementation which explicitly models PV interneurons is expected to show similar behaviour. In such a

likely to lead to overlapping receptive fields of grid cells. The reasons are that afferent information might carry uncertainty that is expressed in a variability of spike times, and that the recurrent inhibition of winner-take-all dynamics, although possibly very fast, is not instantaneous.

To summarize, the function that grid cells provide is knowledge about the spatial relationship between locations. While the identification of transitions occurs on spatially modulated afferents as part of the dendritic computation of grid cells, the information is subsequently conveyed downstream to place cells (see also Figure 8)<sup>20</sup>. The disentanglement of event representation and localization (place cells), temporal transitions, spatial relations (grid cells), and sensory modalities is helpful for planning spatio-temporal trajectories during retrieval operations, in particular shortest or context-modulated paths [98]. Together with place cells and temporal transitions, grid cells form a tripartite graph as illustrated in Figure 6 and, importantly, a *spatio-temporal topological map*.

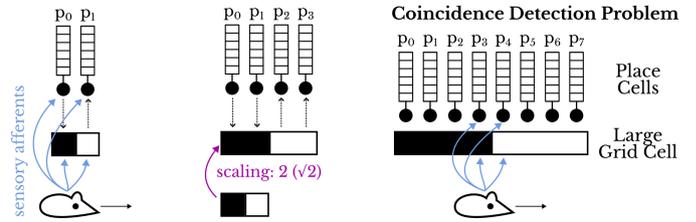
### 3.4 Multiple spatial scales to achieve biologically relevant retrieval times

The system of memories described in the previous sections is sufficient for reproducing sequences and shortest paths. For instance, to retrieve a sequence from  $p$  (current location) to  $r$  (target location), it is sufficient to search the tri-partite connected graph to find a shortest *connected* path from  $p$  to  $r$ . However, it is vital that this computation has a suitable run-time, for instance in the case of a perilous situation<sup>21</sup>. The TSS model uses multiple scales of grid cells to optimally accelerate such retrievals. Each successive scale learns to represent spatial transitions of systematically *increasing* areas, and submits this information downstream to *multiple* place cells.

model, a single PV interneuron would respond to several grid cells, and diffusively all grid cells that it reciprocally connects to in support of spatial transition learning and location disambiguation. This might explain why the responses of single PV interneurons are reminiscent of the cumulative spatial tuning of multiple grid cells [12], and why silencing PV interneurons antagonizes the hexagonal grid response [62].

<sup>20</sup>To convey this information downstream, activity from place cells needs to temporally coincide with the detection of a spatial transition during dendritic computations of grid cells of the TSS model. In other words, detection of a spatial transition is only meaningful in conjunction with the information regarding the *sequential event structure* that they receive from place cells. Still, a population of grid cells needs to be maximally competitive to avoid spurious transitions, which can be implemented with recurrent inhibitory dynamics locally within the population. This observation might explain why real grid cells need drive from Hippocampus to maintain their hexagonal response, but the network maintains coherence even under inactivation of hippocampal afferents [3, 11].

<sup>21</sup>Any neural computation must be fast enough to reach behaviourally relevant performance. This is especially true for the navigation system of a mobile animal. Consider an animal in a perilous situation, such as being chased by a predator, and that the animal cannot rely on visual homing towards a shelter due to obstacles or occlusions. It therefore must compute a solution strategy based exclusively on searching through its memorized locations and how to get from one location to another, until it finds a desired location.



**Figure 8: Simplified illustration of multiple scales of grid cells and the Binding Problem.** (left) A discrete one-dimensional grid cell that learns transitions to its right. The on-center and off-surround area, indicated by the black/white box, is learned on sensory afferents (blue arrows), and the transitional knowledge links place cells, here  $p_0$  and  $p_1$ , which are also recruited from sensory afferents. (middle) Two simplified scales of grid cells, where a grid cell on the smallest scale links place cells  $p_0$  and  $p_1$ , while a grid cell on the next scale links  $(p_0, p_1)$  with  $(p_2, p_3)$ . The optimal scale increment (pink arrow) in the discrete case is 2, and for biologically plausible tuning curves it is  $\sqrt{2}$ . (right) Learning grid cells on larger scales leads to a coincidence detection or *binding problem*. Sensory afferents (blue arrows) are unlikely to activate place cells that are far away from the current location, e.g.  $p_0$  or  $p_7$ . Yet, a large grid cell might need to link these place cells.

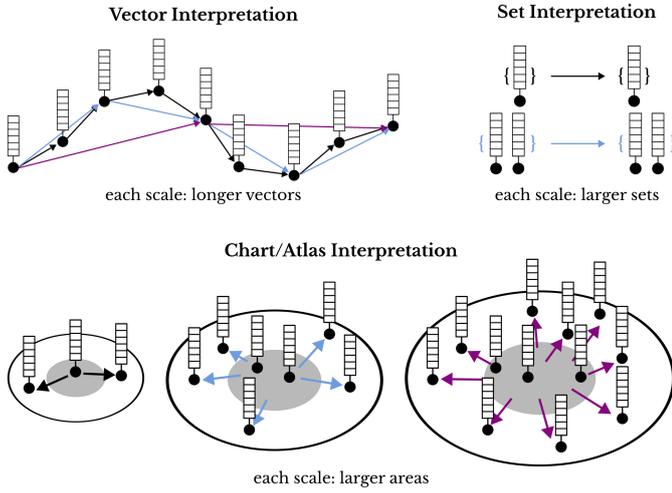
Generally, finding out if a path between two locations exists means to follow all possible trajectories (sequences) outbound from the starting place cell until the target place cell is discovered. In the worst case, however, the search space degenerates to a sequence  $p \rightarrow \dots \rightarrow q_i \rightarrow \dots \rightarrow r$ , where the start location  $p$  and the target location  $r$  are maximally separated by intermediate locations  $q_i$ <sup>22</sup>, and arrows indicate transitions. In this case, the retrieval time is linear in the number of elements on the sequence, which can be prohibitively slow especially under consideration of realistic neural dynamics<sup>23</sup>.

Retrieval times can be accelerated optimally using a search strategy that uses multiple scales of grid modules with a discrete scale increment between successive scales [100]<sup>24</sup>.

<sup>22</sup>In the worst case and without having additional data structures and mechanisms at hand, parallel evaluation of trajectories that are outbound from  $p$  is not a solution. The reason is that the sequence of places from  $p \rightarrow \dots \rightarrow r$  forms what is called the *critical path* of the computation which cannot be reduced any further. In fact, in this case the smallest grid scale and temporal transitions coincide and provide identical information [100].

<sup>23</sup>To further understand the problem of retrieval times, consider the thought experiment where  $p$  and  $r$  are 200 m apart, and each (intermediate) place cell covers an area of 20 cm. Moreover, let the neural dynamics be such that it takes 10 ms per retrieval step to iterate through the place cell and the spatial (or temporal) transition memories. That means that, given one place cell  $q_i$ , it takes 10 ms time to activate the successive place cell  $q_{i+1}$ . Then, retrieving the knowledge that a path between  $p$  and  $r$  exists takes 10 s time. Clearly, any neural navigation system that should be used in realistic scenarios must show significantly better performance.

<sup>24</sup>The optimal acceleration of retrievals is based on and related to *binary search*. The reason for a discrete scale-increment is that, to achieve optimality, binary search requires each successive scale to bisect the entropy that remains in the search space. Under the assumption of discrete grid fields, e.g. rectangular or quadratic fields, the ideal scale increment is 2. The scale increment of 2 is a widely known fact for binary search and finds application in a myriad of applications and data structures, for instance quad-trees, oct-trees, or other search trees that are particularly relevant in high-performance computing or computer graphics.



**Figure 9: Different interpretations of grid cells in the TSS model.** (upper left) Vector interpretation, in which each scale provides a longer vector to accelerate retrievals, indicated by different colours (black: scale 1, blue: scale 2, red: scale 3). Note that this interpretation can be subtly misleading, because transition bundles in the TSS model are not defined on singular points or by magnitude and direction, as in other vector-based navigation models [6]. (upper right) In the set interpretation, spatial transitions on larger scales are mappings between systematically increasing sets. This interpretation emphasizes that place cells lack the knowledge of their spatial (or temporal) relations, which are provided by grid (temporal transition) cells. (bottom) The chart/atlas interpretation combines the vector and set interpretations. Each chart represents spatial transitions from *all* place cells in the on-center to *all* the place cells in the off-surround. Scales are systematically increasing charts, meaning the center/surround regions correspond to increasing chunks of space. This interpretation has a natural connection to differential geometry: each chart provides a local connectivity metric, and multiple charts *stitched* together form an atlas. Note that, in the TSS model, the local metric is learned on the basis of spatially modulated sensory afferents, and the spatial neighborhood relation conveyed downstream to place cells.

The speed-up is exponential with every additional scale<sup>25</sup>, and for biologically plausible receptive field dynamics that follow a Gaussian distribution, the optimal scale increment between modules is  $\sqrt{2}$ . The reason for this particular scale increment is that, for optimally accelerating the search, grid cells on every additional scale need to *double* the area they account for. In turn, this translates to a scale increment of  $\sqrt{2}$  for Gaussian distributions<sup>26</sup>. It follows that both the grid field spacing as well as grid field sizes follow a systematic

<sup>25</sup>Additional information about the structure, relation between, and distribution of places in an environment could lead to further improvements. For instance, so-called kd-trees in computer science use postprocessing steps to partition the data space into segments that depend on the number of points per segment. In the absence of such knowledge and expensive postprocessing, both for which currently no evidence exists in the rodent brain, exponential acceleration as described in the main text is optimal.

<sup>26</sup>Technically, consecutive steps during binary search ideally bisect the remaining entropy in the search space, and thus the area under consideration from one scale to the next needs to follow accordingly. Another mathematical interpretation, in particular for a bottom-up construction, is that each following scale needs to integrate the representations of two grid cells from the previous scale. This integration leads to a convolution of two Gaussian distributions, which has a  $\sqrt{2}$  scale increment in the  $n$ -dimensional case.

increase from one scale to the next. Intuitively, a grid cell on the smallest grid scale learns spatial transitions between the smallest distinguishable areas<sup>27</sup>, meaning it associates with place cells that coincide with the *domain* of a transition (on-center) and projects reciprocally downstream to those place cells that coincide with the *image* (off-surround) of a transition. Grid cells on larger scales learn transitions between larger areas, meaning they associate and project to *all* place cells which coincide with the increased *domain* and *image* of the spatial transition on this scale, respectively<sup>28</sup>.

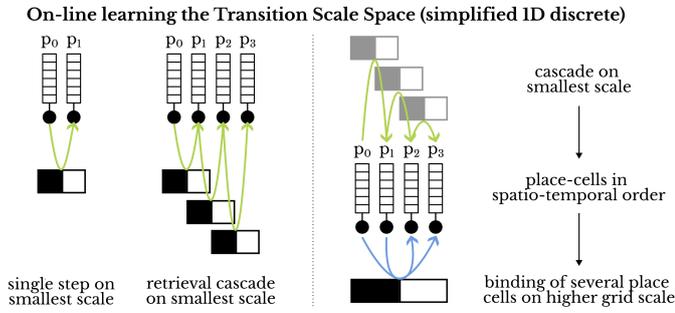
For illustrative purposes, consider one dimensional grid cells with discrete receptive fields that learn transitions to the right on a linear track, as depicted in Figure 8. In this case, grid cells on the second scale learn transitions that start in an area that contains two distinguishable locations, and lead into a region that also covers two locations. In other words, higher scales of grid cells integrate sensory information for larger regions and, thus, provide an abstraction of spatial information to downstream place cells in form of a successive coarsening (or approximation) of spatial relationships. In turn, the approximation can be used to quickly search through the search space. That means that a retrieval process can exploit the approximation that is given by higher scales to quickly find approximate trajectories, and potentially even shortcuts (see the simulated water-maze experiments in [100]). Note, however, that grid fields in the TSS model are in principle independent of the distribution of place cells. That means that they are not formed due to place field afferents, but recruited on spatially modulated inputs such as border cells. Hence, the perfect alignment of grid fields and place cells in Figures 8 and 10 is only due to illustrative simplifications. Rather, grid cells associate with all place cells that coincide with the activity of the grid cell, and thus perform a *pooling* of all coincident place cells. Some further interpretations of the TSS model are illustrated in Figure 9.

To summarize, the collection of multiple grid scales in the TSS model forms a *scale-space of transitions*<sup>29</sup>. The scales follow from acceleration of retrievals, and multiple grid fields per cell are due to bundling multiple transitions. Thus, both the hexagonal distribution of fields and the scale-increment

<sup>27</sup>The smallest scale of grid cells most likely depends on a combination of the presynaptic resolution that is intrinsic to the sensory modalities, and behavioural requirements. Essentially, grid cells need to perform a decoding of the input that they receive to disambiguate and identify locations, but the resolution of the identification should also not exceed behavioural necessities. For instance, it might suffice to identify areas that are approximately the size of 1 or  $1/2$  rodents on the smallest scale, because this could be considered the direct interaction distance of a rodent. An excess resolution could lead to an increase in energy requirements, for instance due to the maintenance of a grid cell population that is larger than behaviourally necessary.

<sup>28</sup>It is important to realize that in the TSS model, grid cells do not operate on singular values but on entire intervals (or areas) of space. This is particularly the case for grid cells on higher grid scales.

<sup>29</sup>Scale-spaces and scale-space theory are widely known concepts in computer vision and models of visual cortex [55], and had a substantial influence during the development of the TSS model.



**Figure 10: On-line learning different grid scales.** Learning large scale grid fields can be achieved using cascaded retrievals from finer grid scales. For instance, given a place cell  $p_0$ , a grid cell on the smallest scale activates the next place cell  $p_1$ . Cascading multiple grid cells on this scale retrieves entire sequences of place cells in spatio-temporal order, for instance  $p_0, \dots, p_3$ . A grid cell on a higher scale can exploit small-scale cascades to *bind*  $p_0$  and  $p_1$  with an on-center field, and convey the relational/transitional information to  $p_2$  and  $p_3$ .

are intrinsic properties of grid cells in the TSS model. This provides a *disentanglement* of representations of events and locations (place cells), and the data structures that are required to represent spatial transitions and to accelerate retrievals (grid cells). However, this disentanglement presents a challenge for learning the acceleration data structure, which will be addressed next.

### 3.5 The temporal dynamics of on-line learning a Transition Scale-Space

In the TSS model, grid cells learn spatial transitions on sensory stimuli, and convey this relational information downstream to place cells. Thereby, they solve a *binding problem* between spatially related place cells. To solve this binding problem for successive scales, grid cells on higher scales need to know which place cells coincide with their spatially modulated receptive grid fields. However, assume that place cells exhibit place fields that are smaller than the grid fields of large grid scales. How can a grid cell on a larger scale learn to associate with the appropriate place cells?

The challenge is to determine the temporal coincidence of place cell activity, and the activity of a grid cell with fields that are larger than place fields. It can be solved by using sufficiently tuned temporal dynamics on each scale of grid cells in combination with exploitation of the smallest grid scale. Consider a one-dimensional grid cell of a large scale with discrete firing fields (see Figure 8). The grid cell's purpose is to establish the knowledge that, on this scale, there is a transition from a region in which  $p_0, \dots, p_3$  are active, to a region in which  $p_4, \dots, p_7$  are active. The problem is that  $p_0$  and  $p_7$  might be far apart from the animal's current location, which means that neither will activate in a timely manner due to lack of sensory stimulation. In turn, this would prevent appropriate synaptic facilitation between the grid and place cells to *bind* them and establish the transitional knowledge. However, this problem can be solved by exploiting smaller grid scales and temporal transitions, as

illustrated in Figure 10. Specifically, it is possible to retrieve one place cell after another using the smallest grid scale. In other words, recursively looping through smaller scales of the spatial transition system activates all place cells in the *spatio-temporal order* they are distributed in real space. The activation of remote place cells that coincide only with larger off-surround grid fields, which indicates the *image* of the transition, is thus driven by local dynamics that are due to the transition system itself, and is independent from sensory stimuli.

Ideally, the iterative retrieval process to learn grid cells on larger scales happens relative to the arrival of sensory stimuli. That means that the iterative retrieval of past and future place cells should be nested within the time-frame that is given by the frequency of sensory data<sup>30</sup>. Interestingly, this allows an interpretation of what is observed during re- and preplay of place cell sequences, and in particular during Theta Phase Precession (TPP) [44]. During TPP, place cells of a navigating animal activate during increasingly earlier phases relative to Theta, and along a linear track relative to the animal's heading direction. The place cell which corresponds most closely to the current location is active in the trough of Theta, whereas past (future) place cells are active *in order* on the downward (upward) slope of the oscillation. This behaviour is precisely the temporal dynamics described above for on-line learning in the TSS model.

Several further predictions follow immediately from the description of online learning of multiple scales in the TSS model. In particular, the temporal dynamics and, transitively, electrophysiological properties are expected to change along the scale of grid cells. Because the time integration windows for grid cells on larger scales must fit to a systematically growing number of place cells that is relative to the spatial increase of the grid fields, the time windows for integration must increase accordingly. In other words, the temporal window should increase in unison with the spatial scale increment. For biologically plausible temporal tuning curves, in particular Difference of Gaussians with shifted centers, the scale increment in the *temporal domain* is again a factor of  $\sqrt{2}$  [100]<sup>31</sup>. It is also possible to approximately predict the number of grid scales that can be expected in real animals based on the temporal dynamics for learning multiple scales [101]. Specifically, it is the number of retrievals of small grid scales that can be nested into one Theta cycle. Under conservative assumptions regarding activation times through the Entorhinal-Hippocampal loop, this number should be in the range of  $7 \pm 2$ . The same number can be established

<sup>30</sup>Computer scientists and roboticists that develop software for embedded systems know this issue quite well. Sensors usually operate at a certain frequency, that is often slower than the frequency of the main processor. Every operation that uses sensory information, such as filtering or postprocessing, must fit into the time-window that is given by the frequency of the sensors.

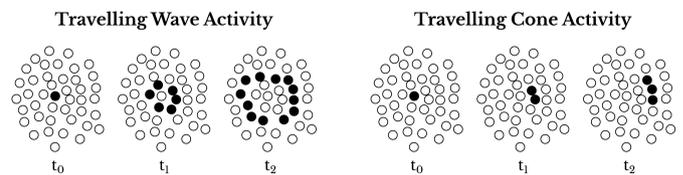
<sup>31</sup>The joint spatio-temporal integration kernels of grid cells of the TSS model have a peculiar similarity to Gabor filters. Gabor filters are a certain type of localized linear filters and widely used in classical models of the primary visual cortex (V1) as well as computer vision [1, 45].

by considering the potential speed-up during retrieval times that each scale provides in awake animals. Specifically, the speed-up becomes negligible relative to the temporal dynamics of real neurons for larger numbers of scales and under normal network operations. As a consequence, this might explain why learning and consolidation of spatial memories is supported by sharp-waves and ripples [43], a temporal effect during which neurons fire at a significantly higher rate than under normal conditions. In addition, note that Theta is not *required* in the TSS model. Retrievals from smaller scales of grid cells is only necessary to establish grid cells on larger scales. Consequently, grid cells on the smallest scale of the TSS model are, in principle, independent of Theta. However, the temporal dynamics that are required for learning multiple grid scales in the TSS model might lead to an explanation of Theta itself. To understand this, consider predicting any future locations that are outbound from the current location using the smallest scale of the TSS model. Without any directional information, this corresponds to a traveling wave of activity, which leads to a steady increase in the number of neurons that activate over time. Even with directional information that narrows down the search direction, maybe provided by head direction cells, it is unlikely that only place cells activate that are on an ideal linear path into the given direction. Stochastic noise, uncertainty in presynaptic information such as the intended heading direction, and other effects that lead to a variability in spike times make it more likely that the search is characterized by a traveling cone. Again, this leads to a steady increase of neurons that activate and, thus, synapses, which should be reflected in the Local Field Potential. The traveling wave and traveling cone are illustrated in Figure 11. Finally, the activation of grid cells along the dorso-ventral axis should reflect the slower temporal dynamics of grid cells on larger scales, and therefore express some form of traveling wave of activity along this axis.

To summarize, the TSS model exploits temporal dynamics to solve the binding problem of place cells and grid cells with large grid fields. The temporal dynamics manifest in retrievals and predictions that are based on smaller grid scales, and are thus an inherent, algorithmic mechanism of the TSS model. Effectively, this leads to the activation of place cells that are along the current trajectory in their spatio-temporal order. Moreover, these temporal dynamics have a striking resemblance of Theta and Theta phase precession.

#### 4 A Roadmap for Future Work

The TSS model is an abstract computational model for grid cells. Some testable predictions that derive from the model were outlined already above, and several more can be found in the original work, in particular regarding predictions for local micro-circuits and heterosynaptic connectivity [98, 100]. The following is a collection of open research questions that follow from the model and its predictions. They form a possible roadmap for future experimental and theoretical



**Figure 11: Travelling wave and cone.** (left) Without directional information, activity in the transition system propagates in form of a wave outbound from the starting place cell (black circle at time step  $t_0$ ). (right) With additional directional information, outbound activity corresponds more likely to a cone due to uncertainty in presynaptic inputs and spike time variability.

work.

- How fast can the Hippocampus stably context-switch between sequences? Due to the abstract nature of the TSS model, it can be extended easily with additional information regarding context or rewards and switch immediately between such. However, it is currently not well established how this might happen in the Hippocampus. Insights will have significant impact in our understanding of reward processing, lead to improved and novel models, and potentially yield further theoretical work on switching sequences in and with dynamical systems. An integral part of this research will be to determine the theoretical stability of systems which can context-switch between different sequences. That means that it will be particularly relevant to determine if such systems accidentally switch to other, related sequences, or if and to which extent one sequence remains stable over multiple cycles of the computation. Further advances in this regard might also have direct impact in artificial systems and robotics, in particular for implementations that use spiking neural networks and exploit the benefits of neuromorphic hardware.
- Can the Hippocampus represent multiple sequences at the same time? Related to the question regarding context, it is currently unclear if there are multiple sequences represented simultaneously in the Hippocampus. However, this could be important in multi-goal tasks, but also for navigational purposes to represent spatial sequences to several remote landmarks, from which ego- and allocentric location can be inferred more accurately than from only one landmark. One variant to represent multiple sequences would be to quickly context-switch between a certain number of sequences, one after the other. Another would be to interleave them *in time* with a certain but systematic time difference relative to each other. A third variant would be to use distinct sub-populations to represent individual sequences to achieve superposition of sequences within the entire network. An implementation of the TSS model using spiking neurons could be an ideal testbed for each hypothesis.
- What is the impact of other hippocampal structures on sequence processing? The TSS model is, so far, only concerned with spatial and temporal events (place cells) and their relations (temporal and spatial transitions).

To increase its utility, reciprocal connectivity with extra-hippocampal and cortical associative areas seems expedient. However, simply reading out the information within the processing loop of the TSS model appears unlikely, given that sequences within the loop might be long and therefore conflict with fast neural temporal dynamics both locally and in receiving areas. That means that the temporal dynamics of real neurons likely require that hippocampal sequences are *chunked* and *compressed* to make them transferrable to associative areas. One particularly interesting candidate to study this is Subiculum, which projects to a variety of areas and exhibits a salient topographical organization [59]. Computational models of other hippocampal structures, such as Subiculum, are thus natural extensions of the TSS model to study sequence chunking and compression.

- What are the computational contributions of place cells in CA1 and CA3? The TSS model contains place cells and temporal transition cells, both of which express place field characteristics. Yet, it is unclear if the model neurons correspond to place cells in CA1 and CA3, or if temporal transition neurons are found in another hippocampal region. To clarify this question, it is imperative to seek further understanding of the *computational purpose* of neurons in CA1 and CA3 during sequence processing. That means that while evidence clearly suggests that place cells in CA1 and CA3 behave differently during familiarization with novel environments [24], their actual computational difference remains elusive. A combination of further rodent experiments that induce remapping in place cells and an improved implementation of the TSS model with accurate temporal dynamics of spiking neurons might provide relevant insights.
- What are the sensory afferents that arrive at grid cells, and how are they integrated? The TSS model assumes only a *suitable* input space. Preliminary simulation results suggest that border cell or boundary vector cell activity is sufficient to reproduce hexagonal fields in square environments. However, it is unclear if there is any form of sensor fusion performed already at an earlier stage, if this happens on the level of individual grid-cells, or the local micro-circuit in which grid cells are embedded? Answers to these questions will allow to make accurate predictions regarding the dense packing of squishy fields and therefore also regarding the distribution of real grid fields, and yield further insights into the performed computations.
- Are there “grid cells” in Lateral Entorhinal Cortex (LEC)? The TSS model predicts that *any* transition system should exhibit fast recurrent inhibition to minimize resources, maximize storage capacity, and avoid spurious transitions. A further prediction of the TSS model is that neurons which bundle multiple transitions might represent transitions for several distinct inputs, as long as these inputs are not adjacent. Curiously, LEC shows striking similarity in functional organization and recurrent inhibition to MEC [68]. Yet, grid cells were not discovered in LEC. Further study of the afferents arriving at LEC might reveal some structure or order in the information they represent. In turn, this might allow to design experiments which gradually sweep through this information space, and thereby elicit grid-like responses in LEC. Given LEC’s involvement in odor processing [53], determining the structure of odor organization, meaning identification of the space of odors and along which axes the representation varies, seems a reasonable starting point.
- Is phase precession between place and grid cells coordinated, and if yes in which way? The TSS model currently uses strong coupling of the temporal dynamics between place and grid cells to solve the binding problem, but weak coupling might be sufficient. Real data could provide insights in particular regarding the formation, size, and stability of both grid and place fields.
- What is the contribution of precise spike timing in grid cells? In the TSS model, precise spike timing is relevant for learning multiple scales, with predictions regarding the temporal integration time windows of grid cells on larger scales. To investigate the impact of precise spike timing in real rodents, the contribution of relative spike times must be analyzed. However, this will require to go significantly beyond most contemporary work on grid cells. Usually, such studies perform correlation analysis on rate maps that wash out the information that is contained within precise spike times. It will also require to record simultaneously from multiple hippocampal areas during a variety of tasks to properly assess the contribution of relative spike times within and across areas.
- How are grid and place cells interconnected on a synaptic level, and how are the local micro-circuits in mEC, CA1, and CA3 functionally organized? The TSS model predicts that transitioning activity from one place cell to another is governed by a combination of presynaptic grid and place cell activity [98]. In fact, grid cells are not considered to be *drivers* of place cell activity, and one way to implement this behaviour is via heterosynaptic connections. Insights into the synaptic connectivity as well as local micro-circuits will further advance our knowledge of the specific computations that are performed.
- What is the behavioural impact of higher grid scales? In the TSS model, grid cells of higher scales are required to accelerate retrievals. If higher scales were silenced, this should be reflected in longer temporal durations that animals take to initiate movements. Effectively, silencing larger grid scales means that preplay of future trajectories will take longer. A challenge during such a silencing study might be other processes which take over in case planning takes too long, for instance switching to a visually driven navigation strategy. Such confounding factors should be avoided using careful study design.
- In which order and shape do connections between cortical

areas, in particular mEC, CA1, and CA3, develop and how strongly are they connected recurrently? This will shed a light on which connectivity patterns are determined due to genetic predisposition, and which follow from local self-organization and tuning. Further information regarding recurrent connectivity will determine to what extent attractor dynamics can be expected.

- How do scales of grid cells self-organize? In the TSS model, multiple scales are a means to accelerate retrievals, but the model does not explain how they originate. Insights into the development and growth of the neural circuits within the Hippocampus will likely shed a light on this process, and lead to new models for the self-organization of grid scales.
- What are the differences between converging and predicting phases during TPP? Where and how do they originate, and is there a difference in functional contribution? In particular, it appears important to determine if there is a fundamental difference between the dynamics of learning and retrieval of sequences, and if this is related to the converging and predicting phases of TPP.
- How many grid cells really exist in the MEC on each scale? The TSS model predicts that the number of grid cells that are required on each scale should decline following an exponential law. This follows from the systematic increase of grid field sizes from one scale to the next, and the exponential speed-up during retrievals per scale. Using conservative numbers of synapses per neuron, the model predicts a number of grid cells on the finest (or smallest) scale that is in the low hundreds, and only tens of neurons on the coarsest scale [101]. This prediction is in line with already available data [91], but further evaluations are required.
- What are the functional contributions of multi-field representations in place cells? Given recent evidence [39, 29], it seems natural to investigate their purpose and incorporate multiple place fields into models.
- How to prevent saturation of the TSS model? In its current form, the TSS model only accumulates information over time. However, a biological system is expected to prune irrelevant information to avoid saturation and to free up resources. It is currently unclear what an optimal pruning strategy would look like, for instance which vertices or edges of the tripartite graph of the TSS model should be removed. Further insight might allow to make predictions regarding forgetting and spatial recency effects in observations from rodents.
- Is there a concise mathematical formulation for (neural) transition systems? The TSS model was derived using propositional logic and first-order principles. Several parts of the model have salient connections to other theories from mathematics, for instance grid cells can be interpreted as functors from category theory [100], but also as differential operators. In particular, grid cells of the

TSS model operate on two spaces with different *types* at the same time, similar to functors, but relay transitional information, meaning a change in the space, similar to differential operators. It remains for future work to investigate if there is a concise mathematical framework, maybe based on *type theory*, that captures these similarities.

## 5 Summary

This paper reviewed the TSS model for grid cells. The model suggests distinct functionalities for place and grid cells in the Entorhinal-Hippocampal loop. While place cells are proposed to perform localization both in space and time, grid cells learn spatial transitions, meaning the spatial structure and relation between places. The model explains hexagonally distributed grid fields as a result of optimally representing spatial transitions, and a discrete scale increment of grid fields with a factor of  $\sqrt{2}$  as a consequence of optimally accelerating retrievals of sequences. Moreover, learning the eponymous *scale-space of transitions* in an online fashion induces temporal dynamics that match Theta phase precession.

The article provided an intuitive and accessible introduction to the TSS model, and contrasted it with other existing models from the literature. Several testable predictions were derived from the TSS model, and open research questions listed which provide a roadmap for future experimental and theoretical research.

## References

- [1] Edward H. Adelson and James R. Bergen. "Spatiotemporal Energy Models for the Perception of Motion". In: *Journal of the Optical Society of America A* 2.2 (Feb. 1, 1985), p. 284. ISSN: 1084-7529, 1520-8532. DOI: 10.1364/JOSAA.2.000284.
- [2] Haggai Agmon and Yoram Burak. "A Theory of Joint Attractor Dynamics in the Hippocampus and the Entorhinal Cortex Accounts for Artificial Remapping and Grid Cell Field-to-Field Variability". In: *eLife* 9 (Aug. 11, 2020), e56894. ISSN: 2050-084X. DOI: 10.7554/eLife.56894.
- [3] Noam Almog et al. "During Hippocampal Inactivation, Grid Cells Maintain Synchrony, Even When the Grid Pattern Is Lost". In: *eLife* 8 (Oct. 17, 2019), e47147. ISSN: 2050-084X. DOI: 10.7554/eLife.47147.
- [4] Daniel J Amit, Hanoch Gutfreund, and H Sompolinsky. "Statistical Mechanics of Neural Networks near Saturation". In: *Annals of Physics* 173.1 (Jan. 1987), pp. 30–67. ISSN: 00034916. DOI: 10.1016/0003-4916(87)90092-3.
- [5] Per Andersen. "Organization of Hippocampal Neurons and Their Interconnections". In: *The Hippocampus*. Springer US, 1975, pp. 155–175. DOI: 10.1007/978-1-4684-2976-3\_7.
- [6] Andrea Banino et al. "Vector-Based Navigation Using Grid-like Representations in Artificial Agents". In: *Nature* 557.7705 (May 2018), pp. 429–433. ISSN: 0028-0836, 1476-4687. DOI: 10.1038/s41586-018-0102-6.
- [7] Jean-Paul Banquet et al. "Time as the Fourth Dimension in the Hippocampus". In: *Progress in Neurobiology* 199 (Apr. 2021), p. 101920. ISSN: 03010082. DOI: 10.1016/j.pneurobio.2020.101920.

- [8] C. Barry et al. “The Boundary Vector Cell Model of Place Cell Firing and Spatial Memory”. In: *Reviews in the Neurosciences* 17.1-2 (Jan. 2006). ISSN: 2191-0200, 0334-1763. DOI: 10.1515/REVNEURO.2006.17.1-2.71.
- [9] Edgar Bermudez-Contreras, Benjamin J. Clark, and Aaron Wilber. “The Neuroscience of Spatial Navigation and the Relationship to Artificial Intelligence”. In: *Frontiers in Computational Neuroscience* 14 (July 28, 2020), p. 63. ISSN: 1662-5188. DOI: 10.3389/fncom.2020.00063.
- [10] Tale L. Bjercknes, Edvard I. Moser, and May-Britt Moser. “Representation of Geometric Borders in the Developing Rat”. In: *Neuron* 82.1 (Apr. 2014), pp. 71–78. ISSN: 08966273. DOI: 10.1016/j.neuron.2014.02.014.
- [11] Tora Bonnevie et al. “Grid Cells Require Excitatory Drive from the Hippocampus”. In: *Nature Neuroscience* 16.3 (Mar. 2013), pp. 309–317. ISSN: 1097-6256, 1546-1726. DOI: 10.1038/nn.3311.
- [12] Christina Buetfering, Kevin Allen, and Hannah Monyer. “Parvalbumin Interneurons Provide Grid Cell-Driven Recurrent Inhibition in the Medial Entorhinal Cortex”. In: *Nature Neuroscience* 17.5 (May 2014), pp. 710–718. ISSN: 1097-6256, 1546-1726. DOI: 10.1038/nn.3696.
- [13] Yoram Burak and Ila R. Fiete. “Accurate Path Integration in Continuous Attractor Network Models of Grid Cells”. In: *PLoS Computational Biology* 5.2 (Feb. 20, 2009). Ed. by Olaf Sporns, e1000291. ISSN: 1553-7358. DOI: 10.1371/journal.pcbi.1000291.
- [14] Neil Burgess, Caswell Barry, and John O’Keefe. “An Oscillatory Interference Model of Grid Cell Firing”. In: *Hippocampus* 17.9 (Sept. 2007), pp. 801–812. ISSN: 10509631, 10981063. DOI: 10.1002/hipo.20327.
- [15] Daniel Bush and Christoph Schmidt-Hieber. “Computational Models of Grid Cell Firing”. In: *Hippocampal Microcircuits*. Ed. by Vassilis Cutsuridis et al. Springer Series in Computational Neuroscience. Cham: Springer International Publishing, 2018, pp. 585–613. ISBN: 978-3-319-99103-0. DOI: 10.1007/978-3-319-99103-0\_16.
- [16] Jonathan J Couey et al. “Recurrent Inhibitory Circuitry as a Mechanism for Grid Formation”. In: *Nature Neuroscience* 16.3 (Mar. 2013), pp. 318–324. ISSN: 1097-6256, 1546-1726. DOI: 10.1038/nn.3310.
- [17] Michael Cross and Henry Greenside. *Pattern Formation and Dynamics in Nonequilibrium Systems*. 1st ed. Cambridge University Press, 2009. 552 pp. ISBN: 0-521-77050-5.
- [18] Christopher J Cueva and Xue-Xin Wei. “Emergence of Grid-like Representations by Training Recurrent Neural Networks to Perform Spatial Localization”. In: International Conference for Learning Representations. 2018, p. 19.
- [19] N. Cuperlier et al. “Transition Cells for Navigation and Planning in an Unknown Environment”. In: *From Animals to Animals 9*. Ed. by Stefano Nolfi et al. Red. by David Hutchison et al. Vol. 4095. Lecture Notes in Computer Science. Berlin, Heidelberg: Springer Berlin Heidelberg, 2006, pp. 286–297. ISBN: 978-3-540-38608-7. DOI: 10.1007/11840541\_24.
- [20] Nicolas Cuperlier. “Neurobiologically Inspired Mobile Robot Navigation and Planning”. In: *Frontiers in Neurobotics* 1 (2007). ISSN: 1662-5218. DOI: 10.3389/neuro.12.003.2007.
- [21] Y. Dabaghian et al. “A Topological Paradigm for Hippocampal Spatial Map Formation Using Persistent Homology”. In: *PLoS Computational Biology* 8.8 (Aug. 9, 2012). Ed. by Ila Fiete, e1002581. ISSN: 1553-7358. DOI: 10.1371/journal.pcbi.1002581.
- [22] Yuri Dabaghian, Vicky L Brandt, and Loren M Frank. “Reconceiving the Hippocampal Map as a Topological Template”. In: *eLife* 3 (Aug. 20, 2014), e03476. ISSN: 2050-084X. DOI: 10.7554/eLife.03476.
- [23] Dori Derdikman et al. “Fragmentation of Grid Cell Maps in a Multicompartment Environment”. In: *Nature Neuroscience* 12.10 (Oct. 2009), pp. 1325–1332. ISSN: 1097-6256, 1546-1726. DOI: 10.1038/nn.2396.
- [24] Can Dong, Antoine D. Madar, and Mark E. J. Sheffield. “Distinct Place Cell Dynamics in CA1 and CA3 Encode Experience in New Environments”. In: *Nature Communications* 12.1 (Dec. 2021), p. 2977. ISSN: 2041-1723. DOI: 10.1038/s41467-021-23260-3.
- [25] Yedidyah Dordek et al. “Extracting Grid Cell Characteristics from Place Cell Inputs Using Non-Negative Principal Component Analysis”. In: *eLife* 5 (Mar. 8, 2016), e10094. ISSN: 2050-084X. DOI: 10.7554/eLife.10094.
- [26] George Dragoi and Susumu Tonegawa. “Preplay of Future Place Cell Sequences by Hippocampal Cellular Assemblies”. In: *Nature* 469.7330 (Jan. 2011), pp. 397–401. ISSN: 0028-0836, 1476-4687. DOI: 10.1038/nature09633.
- [27] Vegard Edvardsen. “Navigating with Distorted Grid Cells”. In: *The 2018 Conference on Artificial Life*. The 2018 Conference on Artificial Life. Tokyo, Japan: MIT Press, 2018, pp. 260–267. DOI: 10.1162/isal\_a\_00053.
- [28] Vegard Edvardsen, Andrej Bicanski, and Neil Burgess. “Navigating with Grid and Place Cells in Cluttered Environments”. In: *Hippocampus* 30.3 (2020), pp. 220–232. ISSN: 1098-1063. DOI: 10.1002/hipo.23147.
- [29] Tamir Eliav et al. “Multiscale Representation of Very Large Environments in the Hippocampus of Flying Bats”. In: *Science* 372.6545 (May 28, 2021), eabg4020. ISSN: 0036-8075, 1095-9203. DOI: 10.1126/science.abg4020.
- [30] Ugur M. Erdem and Michael E. Hasselmo. “A biologically inspired hierarchical goal directed navigation model”. In: *J. Physiol. Paris* 108.1 (Feb. 2014), pp. 28–37.
- [31] Ugur M. Erdem, Michael J. Milford, and Michael E. Hasselmo. “A hierarchical model of goal directed navigation selects trajectories in a visual environment”. In: *Neurobiology of Learning and Memory* 117 (2015). Memory and decision making, pp. 109–121. ISSN: 1074-7427. DOI: <http://dx.doi.org/10.1016/j.nlm.2014.07.003>.
- [32] M. C. Fuhs. “A Spin Glass Model of Path Integration in Rat Medial Entorhinal Cortex”. In: *Journal of Neuroscience* 26.16 (Apr. 19, 2006), pp. 4266–4276. ISSN: 0270-6474, 1529-2401. DOI: 10.1523/JNEUROSCI.4353-05.2006.
- [33] Richard J. Gardner et al. “Toroidal topology of population activity in grid cells”. In: *Nature* 602.7895 (Jan. 2022), pp. 123–128. DOI: 10.1038/s41586-021-04268-7.
- [34] Gily Ginosar et al. “Locally Ordered Representation of 3D Space in the Entorhinal Cortex”. In: *Nature* 596.7872 (Aug. 19, 2021), pp. 404–409. ISSN: 0028-0836, 1476-4687. DOI: 10.1038/s41586-021-03783-x.
- [35] Lisa M. Giocomo, May-Britt Moser, and Edvard I. Moser. “Computational Models of Grid Cells”. In: *Neuron* 71.4 (Aug. 2011), pp. 589–603. ISSN: 08966273. DOI: 10.1016/j.neuron.2011.07.023.
- [36] Tim Gollisch and Markus Meister. “Rapid Neural Coding in the Retina with Relative Spike Latencies”. In: *Science* 319.5866 (Feb. 22, 2008), pp. 1108–1111. ISSN: 0036-8075, 1095-9203. DOI: 10.1126/science.1149639.
- [37] Roddy M. Grieves et al. “Irregular Distribution of Grid Cell Firing Fields in Rats Exploring a 3D Volumetric Space”. In: *Nature Neuroscience* (Aug. 11, 2021). ISSN: 1097-6256, 1546-1726. DOI: 10.1038/s41593-021-00907-4.
- [38] Torkel Hafting et al. “Microstructure of a spatial map in the entorhinal cortex”. In: *Nature* 436.7052 (Aug. 2005), pp. 801–806. ISSN: 0028-0836. DOI: 10.1038/nature03721.
- [39] B.C. Harland et al. *Dorsal CA1 Hippocampal Place Cells Form a Multi-Scale Representation of Megaspace*. preprint. Neuroscience, Feb. 16, 2021. DOI: 10.1101/2021.02.15.431172.
- [40] Michael E. Hasselmo. “Grid Cell Mechanisms and Function: Contributions of Entorhinal Persistent Spiking and Phase Resetting”. In: *Hippocampus* 18.12 (Dec. 2008), pp. 1213–1229. ISSN: 10509631, 10981063. DOI: 10.1002/hipo.20512.

- [41] Julien Hirel et al. “Why and How Hippocampal Transition Cells Can Be Used in Reinforcement Learning”. In: *From Animals to Animals 11: 11th International Conference on Simulation of Adaptive Behavior, SAB 2010, Paris - Clos Lucé, France, August 25-28, 2010. Proceedings*. Ed. by Stéphane Doncieux et al. Berlin, Heidelberg: Springer Berlin Heidelberg, 2010, pp. 359–369. ISBN: 978-3-642-15193-4. DOI: 10.1007/978-3-642-15193-4\_34.
- [42] Bernhard Hofmann-Wellenhof, Klaus Legat, and Manfred Wieser. *Navigation*. Vienna: Springer Vienna, 2003. ISBN: 978-3-7091-6078-7. DOI: 10.1007/978-3-7091-6078-7.
- [43] Shantanu P. Jadhav et al. “Awake Hippocampal Sharp-Wave Ripples Support Spatial Memory”. In: *Science* 336.6087 (2012), pp. 1454–1458. ISSN: 0036-8075. DOI: 10.1126/science.1217230.
- [44] Jorge Jaramillo and Richard Kempster. “Phase Precession: A Neural Code Underlying Episodic Memory?” In: *Current Opinion in Neurobiology* 43 (Apr. 2017), pp. 130–138. ISSN: 09594388. DOI: 10.1016/j.conb.2017.02.006.
- [45] J. P. Jones and L. A. Palmer. “An Evaluation of the Two-Dimensional Gabor Filter Model of Simple Receptive Fields in Cat Striate Cortex”. In: *Journal of Neurophysiology* 58.6 (Dec. 1, 1987), pp. 1233–1258. ISSN: 0022-3077, 1522-1598. DOI: 10.1152/jn.1987.58.6.1233.
- [46] Clifford Kentros. “Hippocampal Place Cells: The “Where” of Episodic Memory?” In: *Hippocampus* 16.9 (Sept. 2006), pp. 743–754. ISSN: 1050-9631, 1098-1063. DOI: 10.1002/hipo.20199.
- [47] Emilio Kropff and Alessandro Treves. “The Emergence of Grid Cells: Intelligent Design or Just Adaptation?” In: *Hippocampus* 18.12 (Dec. 2008), pp. 1256–1269. ISSN: 10509631, 10981063. DOI: 10.1002/hipo.20520.
- [48] Dmitry Krotov and John J. Hopfield. “Dense Associative Memory for Pattern Recognition”. In: *Advances in Neural Information Processing Systems*. Vol. 29. Curran Associates, Inc., 2016.
- [49] J. Krupic, N. Burgess, and J. O’Keefe. “Neural Representations of Location Composed of Spatially Periodic Bands”. In: *Science* 337.6096 (Aug. 17, 2012), pp. 853–857. ISSN: 0036-8075, 1095-9203. DOI: 10.1126/science.1222403.
- [50] Julija Krupic et al. “Grid Cell Symmetry Is Shaped by Environmental Geometry”. In: *Nature* 518.7538 (Feb. 2015), pp. 232–235. ISSN: 0028-0836, 1476-4687. DOI: 10.1038/nature14153.
- [51] Julija Krupic et al. “How Environment Geometry Affects Grid Cell Symmetry and What We Can Learn from It”. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 369.1635 (Feb. 5, 2014), p. 20130188. ISSN: 0962-8436, 1471-2970. DOI: 10.1098/rstb.2013.0188.
- [52] John L. Kubie and André A. Fenton. “Linear look-ahead in conjunctive cells: an entorhinal mechanism for vector-based navigation”. In: *Front Neural Circuits* 6 (2012), p. 20.
- [53] Frauke C Leitner et al. “Spatially Segregated Feedforward and Feedback Neurons Support Differential Odor Processing in the Lateral Entorhinal Cortex”. In: *Nature Neuroscience* 19.7 (July 2016), pp. 935–944. ISSN: 1097-6256, 1546-1726. DOI: 10.1038/nn.4303.
- [54] C. Lever et al. “Boundary Vector Cells in the Subiculum of the Hippocampal Formation”. In: *Journal of Neuroscience* 29.31 (Aug. 5, 2009), pp. 9771–9777. ISSN: 0270-6474, 1529-2401. DOI: 10.1523/JNEUROSCI.1319-09.2009.
- [55] Tony Lindeberg. *Scale-Space Theory in Computer Vision*. Boston, MA: Springer US, 1994. ISBN: 978-1-4419-5139-7. DOI: 10.1007/978-1-4757-6465-9.
- [56] Wolfgang Maass. “On the Computational Power of Winner-Take-All”. In: *Neural Computation* 12.11 (Nov. 1, 2000), pp. 2519–2535. ISSN: 0899-7667, 1530-888X. DOI: 10.1162/089976600300014827.
- [57] David Marr. *Vision: A Computational Investigation into the Human Representation and Processing of Visual Information*. W.H. Freeman, 1982. 397 pp.
- [58] Alexander Mathis, Andreas V. M. Herz, and Martin B. Stemmler. “Resolution of Nested Neuronal Representations Can Be Exponential in the Number of Neurons”. In: *Physical Review Letters* 109.1 (July 6, 2012), p. 018103. ISSN: 0031-9007, 1079-7114. DOI: 10.1103/PhysRevLett.109.018103.
- [59] Nobuyoshi Matsumoto, Takuma Kitanishi, and Kenji Mizuseki. “The Subiculum: Unique Hippocampal Hub and More”. In: *Neuroscience Research* 143 (June 2019), pp. 1–12. ISSN: 01680102. DOI: 10.1016/j.neures.2018.08.002.
- [60] Bruce L. McNaughton et al. “Path Integration and the Neural Basis of the ‘Cognitive Map’”. In: *Nature Reviews Neuroscience* 7.8 (Aug. 2006), pp. 663–678. ISSN: 1471-003X, 1471-0048. DOI: 10.1038/nrn1932.
- [61] Himanshu Mhatre, Anatoli Gorchetchnikov, and Stephen Grossberg. “Grid Cell Hexagonal Patterns Formed by Fast Self-Organized Learning within Entorhinal Cortex”. In: *Hippocampus* 22.2 (Feb. 2012), pp. 320–334. ISSN: 10509631. DOI: 10.1002/hipo.20901.
- [62] Chenglin Miao et al. “Parvalbumin and Somatostatin Interneurons Control Different Space-Coding Networks in the Medial Entorhinal Cortex”. In: *Cell* 171.3 (Oct. 2017), 507–521.e17. ISSN: 00928674. DOI: 10.1016/j.cell.2017.08.050.
- [63] Michael Milford et al. “RatSLAM: Using Models of Rodent Hippocampus for Robot Navigation and Beyond”. In: *Robotics Research*. Ed. by Masayuki Inaba and Peter Corke. Vol. 114. Springer Tracts in Advanced Robotics. Cham: Springer International Publishing, 2016, pp. 467–485. ISBN: 978-3-319-28872-7. DOI: 10.1007/978-3-319-28872-7\_27.
- [64] Genela Morris and Dori Derdikman. “The Chicken and Egg Problem of Grid Cells and Place Cells”. In: *Trends in Cognitive Sciences* (Nov. 2022), S1364661322002832. ISSN: 13646613. DOI: 10.1016/j.tics.2022.11.003.
- [65] Edvard I Moser, May-Britt Moser, and Bruce L McNaughton. “Spatial Representation in the Hippocampal Formation: A History”. In: *Nature Neuroscience* 20.11 (Nov. 2017), pp. 1448–1464. ISSN: 1097-6256, 1546-1726. DOI: 10.1038/nn.4653.
- [66] Marcello Mulas, Nicolai Waniek, and Jörg Conradt. “Hebbian Plasticity Realigns Grid Cell Activity with External Sensory Cues in Continuous Attractor Models”. In: *Frontiers in Computational Neuroscience* 10 (Feb. 17, 2016). ISSN: 1662-5188. DOI: 10.3389/fncom.2016.00013.
- [67] Chi T. Ngo et al. “Pattern Separation and Pattern Completion: Behaviorally Separable Processes?” In: *Memory & Cognition* 49.1 (Jan. 2021), pp. 193–205. ISSN: 0090-502X, 1532-5946. DOI: 10.3758/s13421-020-01072-y.
- [68] Eirik S. Nilssen et al. “Neurons and Networks in the Entorhinal Cortex: A Reappraisal of the Lateral and Medial Entorhinal Subdivisions Mediating Parallel Cortical Pathways”. In: *Hippocampus* 29.12 (Dec. 2019), pp. 1238–1254. ISSN: 1050-9631, 1098-1063. DOI: 10.1002/hipo.23145.
- [69] J. O’Keefe and J. Dostrovsky. “The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat”. In: *Brain Research* 34.1 (1971), pp. 171–175. ISSN: 0006-8993. DOI: [http://dx.doi.org/10.1016/0006-8993\(71\)90358-1](http://dx.doi.org/10.1016/0006-8993(71)90358-1).
- [70] John O’Keefe and Lynn Nadel. *The Hippocampus as a Cognitive Map*. Oxford: New York: Clarendon Press; Oxford University Press, 1978. 570 pp. ISBN: 978-0-19-857206-0.
- [71] H Freyja Ólafsdóttir, Francis Carpenter, and Caswell Barry. “Coordinated Grid and Place Cell Replay during Rest”. In: *Nature Neuroscience* 19.6 (June 2016), pp. 792–794. ISSN: 1097-6256, 1546-1726. DOI: 10.1038/nn.4291.
- [72] G. Palm. “On Associative Memory”. In: *Biological Cybernetics* 36.1 (1980), pp. 19–31. ISSN: 0340-1200, 1432-0770. DOI: 10.1007/BF00337019.

- [73] G. Palm. “On the Asymptotic Information Storage Capacity of Neural Networks”. In: *Neural Computers*. Ed. by Rolf Eckmiller and Christoph v.d. Malsburg. Berlin, Heidelberg: Springer Berlin Heidelberg, 1989, pp. 271–280. ISBN: 978-3-642-83740-1.
- [74] Günther Palm. “Neural Associative Memories and Sparse Coding”. In: *Neural Networks 37* (Jan. 2013), pp. 165–171. ISSN: 08936080. DOI: 10.1016/j.neunet.2012.08.013.
- [75] Brad E. Pfeiffer and David J. Foster. “Hippocampal Place-Cell Sequences Depict Future Paths to Remembered Goals”. In: *Nature* 497.7447 (May 2013), pp. 74–79. ISSN: 0028-0836, 1476-4687. DOI: 10.1038/nature12112.
- [76] Praveen K. Pilly and Stephen Grossberg. “How Does the Modular Organization of Entorhinal Grid Cells Develop?” In: *Frontiers in Human Neuroscience* 8 (June 3, 2014). ISSN: 1662-5161. DOI: 10.3389/fnhum.2014.00337.
- [77] J. B. Ranck. “Head-direction cells in the deep cell layers of dorsal presubiculum in freely moving rats”. In: *Society for Neuroscience Abstracts* 10 (1984).
- [78] A. David Redish et al. *Navigating with Landmarks: Computing Goal Locations from Place Codes*. 1996.
- [79] Edmund T. Rolls. “The Mechanisms for Pattern Completion and Pattern Separation in the Hippocampus”. In: *Frontiers in Systems Neuroscience* 7 (2013). ISSN: 1662-5137. DOI: 10.3389/fnsys.2013.00074.
- [80] Francesco Savelli and James J. Knierim. “Origin and Role of Path Integration in the Cognitive Representations of the Hippocampus: Computational Insights into Open Questions”. In: *Journal of Experimental Biology* 222 (Suppl\_1 Feb. 6, 2019). Ed. by Basil el Jundi, Almut Kelber, and Barbara Webb, jeb188912. ISSN: 1477-9145, 0022-0949. DOI: 10.1242/jeb.188912.
- [81] Rylan Schaeffer, Mikail Khona, and Ila Rani Fiete. “No Free Lunch from Deep Learning in Neuroscience: A Case Study through Models of the Entorhinal-Hippocampal Circuit”. In: 39th International Conference on Machine Learning, 2nd AI4Science Workshop, 2022. DOI: 10.1101/2022.08.07.503109.
- [82] F. Schwenker, F.T. Sommer, and G. Palm. “Iterative Retrieval of Sparsely Coded Associative Memory Patterns”. In: *Neural Networks* 9.3 (Apr. 1996), pp. 445–455. ISSN: 08936080. DOI: 10.1016/0893-6080(95)00112-3.
- [83] W. E. Skaggs and B. L. McNaughton. “Replay of Neuronal Firing Sequences in Rat Hippocampus During Sleep Following Spatial Experience”. In: *Science* 271.5257 (Mar. 29, 1996), pp. 1870–1873. ISSN: 0036-8075, 1095-9203. DOI: 10.1126/science.271.5257.1870.
- [84] David M. Smith and Sheri J.Y. Mizumori. “Hippocampal Place Cells, Context, and Episodic Memory”. In: *Hippocampus* 16.9 (2006), pp. 716–729. ISSN: 1098-1063. DOI: 10.1002/hipo.20208.
- [85] Hansem Sohn and Devika Narain. “Neural Implementations of Bayesian Inference”. In: *Current Opinion in Neurobiology* 70 (Oct. 2021), pp. 121–129. ISSN: 09594388. DOI: 10.1016/j.conb.2021.09.008.
- [86] Ben Sorscher et al. “A Unified Theory for the Origin of Grid Cells through the Lens of Pattern Formation”. In: *Advances in Neural Information Processing Systems*. Ed. by H. Wallach et al. Vol. 32. Curran Associates, Inc., 2019.
- [87] Ben Sorscher et al. *When and Why Grid Cells Appear or Not in Trained Path Integrators*. preprint. Neuroscience, Nov. 15, 2022. DOI: 10.1101/2022.11.14.516537.
- [88] Kimberly L Stachenfeld, Matthew M Botvinick, and Samuel J Gershman. “The Hippocampus as a Predictive Map”. In: *Nature Neuroscience* 20.11 (Nov. 1, 2017), pp. 1643–1653. ISSN: 1097-6256, 1546-1726. DOI: 10.1038/nn.4650.
- [89] Bernhard P Staresina et al. “Hippocampal Pattern Completion Is Linked to Gamma Power Increases and Alpha Power Decreases during Recollection”. In: *eLife* 5 (Aug. 10, 2016), e17397. ISSN: 2050-084X. DOI: 10.7554/eLife.17397.
- [90] Martin Stemmler, Alexander Mathis, and Andreas V. M. Herz. “Connecting Multiple Spatial Scales to Decode the Population Activity of Grid Cells”. In: *Science Advances* 1.11 (Dec. 2015), e1500816. ISSN: 2375-2548. DOI: 10.1126/science.1500816.
- [91] Hanne Stensola et al. “The entorhinal grid map is discretized”. In: *Nature* 492.7427 (Dec. 2012), pp. 72–78. ISSN: 0028-0836. DOI: 10.1038/nature11649.
- [92] Tor Stensola et al. “Shearing-Induced Asymmetry in Entorhinal Grid Cells”. In: *Nature* 518.7538 (Feb. 2015), pp. 207–212. ISSN: 0028-0836, 1476-4687. DOI: 10.1038/nature14151.
- [93] Js Taube, Ru Muller, and Jb Ranck. “Head-Direction Cells Recorded from the Postsubiculum in Freely Moving Rats. I. Description and Quantitative Analysis”. In: *The Journal of Neuroscience* 10.2 (Feb. 1, 1990), pp. 420–435. ISSN: 0270-6474, 1529-2401. DOI: 10.1523/JNEUROSCI.10-02-00420.1990.
- [94] Timothy J. Teyler and Pascal DiScenna. “The Hippocampal Memory Indexing Theory.” In: *Behavioral Neuroscience* 100.2 (1986), p. 147. ISSN: 1939-0084. DOI: 10.1037/0735-7044.100.2.147.
- [95] Timothy J. Teyler and Jerry W. Rudy. “The Hippocampal Indexing Theory and Episodic Memory: Updating the Index”. In: *Hippocampus* 17.12 (Dec. 2007), pp. 1158–1169. ISSN: 10509631, 10981063. DOI: 10.1002/hipo.20350.
- [96] Edward C. Tolman. “Cognitive Maps in Rats and Men.” In: *Psychological Review* 55.4 (1948), pp. 189–208. ISSN: 1939-1471, 0033-295X. DOI: 10.1037/h0061626.
- [97] Alan M. Turing. “The Chemical Basis of Morphogenesis”. In: Series B 237.641 (1952).
- [98] Nicolai Waniek. “Hexagonal Grid Fields Optimally Encode Transitions in Spatiotemporal Sequences”. In: *Neural Computation* 30.10 (Oct. 2018), pp. 2691–2725. ISSN: 0899-7667, 1530-888X. DOI: 10.1162/neco\_a\_01122.
- [99] Nicolai Waniek. *Multi-Transition Systems: A Theory for Neural Spatial Navigation*. preprint. Neuroscience, Aug. 10, 2017. DOI: 10.1101/174946.
- [100] Nicolai Waniek. “Transition Scale-Spaces: A Computational Theory for the Discretized Entorhinal Cortex”. In: *Neural Computation* 32.2 (Feb. 2020), pp. 330–394. ISSN: 0899-7667, 1530-888X. DOI: 10.1162/neco\_a\_01255.
- [101] Nicolai Sebastian Waniek. “Locally Distributed Spatial Navigation in a Scale-Space Model for Grid Cells”. PhD thesis. Munich, Germany: Technical University of Munich, 2018. 175 pp.
- [102] Xue-Xin Wei, Jason Prentice, and Vijay Balasubramanian. “The Sense of Place: Grid Cells in the Brain and the Transcendental Number e”. In: *eLife* 4 (Sept. 3, 2015), e08362. ISSN: 2050-084X. DOI: 10.7554/eLife.08362. arXiv: 1304.0031.
- [103] A. C. Welday et al. “Cosine Directional Tuning of Theta Cell Burst Frequencies: Evidence for Spatial Coding by Oscillatory Interference”. In: *Journal of Neuroscience* 31.45 (Nov. 9, 2011), pp. 16157–16176. ISSN: 0270-6474, 1529-2401. DOI: 10.1523/JNEUROSCI.0712-11.2011.
- [104] Thomas Wennekers and Günther Palm. “Controlling the Speed of Synfire Chains”. In: *Artificial Neural Networks – ICANN 96*. Ed. by Christoph von der Malsburg et al. Berlin, Heidelberg: Springer Berlin Heidelberg, 1996, pp. 451–456. ISBN: 978-3-540-68684-2.
- [105] Thomas Wennekers and Günther Palm. “Syntactic Sequencing in Hebbian Cell Assemblies”. In: *Cognitive Neurodynamics* 3.4 (Dec. 2009), pp. 429–441. ISSN: 1871-4080, 1871-4099. DOI: 10.1007/s11571-009-9095-z.
- [106] James C. R. Whittington et al. “How to Build a Cognitive Map”. In: *Nature Neuroscience* 25.10 (Oct. 2022), pp. 1257–1272. ISSN: 1097-6256, 1546-1726. DOI: 10.1038/s41593-022-01153-y.

- [107] James C.R. Whittington et al. “The Tolman-Eichenbaum Machine: Unifying Space and Relational Memory through Generalization in the Hippocampal Formation”. In: *Cell* 183.5 (Nov. 2020), 1249–1263.e23. ISSN: 00928674. DOI: 10.1016/j.cell.2020.10.024.
- [108] Kijung Yoon et al. “Specific Evidence of Low-Dimensional Continuous Attractor Dynamics in Grid Cells”. In: *Nature Neuroscience* 16.8 (Aug. 2013), pp. 1077–1084. ISSN: 1097-6256, 1546-1726. DOI: 10.1038/nn.3450.
- [109] Eric A. Zilli. “Models of Grid Cell Spatial Firing Published 2005 – 2011”. In: *Frontiers in Neural Circuits* 6 (2012). ISSN: 1662-5110. DOI: 10.3389/fncir.2012.00016.