Modelling Environmental and Self-motion Influences on Grid Cell Firing

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I, Talfan Evans confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.
ABSTRACT

Grid cells have been suggested to play a role in path integration, the process of integrating self-motion cues in order to maintain an estimate of location relative to a previous estimate. However, a system performing pure path integration will integrate error such that the estimate of location will drift over time. In contrast, grid cells are known to be stable over time suggesting that they are stabilized by sensory inputs from their environment. Together with their striking anatomical arrangement, this observation also suggests that grid cells may constitute an efficient encoding of space that might be useful for localization or navigation over large distances.

However, distortions to the canonical hexagonal pattern have been observed in large \cite{Stensola:2015} or non-rectangular \cite{Derdikman:2009,Krupic:2015} environments. The same firing patterns are also known to be non-stationary over time, temporarily rescaling in novel environments \cite{Barry:2012}, rescaling in response to environmental manipulations \cite{Barry:2007,Stensola:2012,Krupic:2018}, undergoing a shear-like transformation and re-alignment with experience of a square box \cite{Stensola:2015,Krupic:2015} and adjusting local representations to reflect global structure \cite{Carpenter:2015}.

Sensory input to grid cells is thought to be mediated by place cells or boundary vector cells found in areas CA1/3 of the hippocampus and subiculum, respectively. Existing models rely on strong stimuli from pre-learned associations with these sensory inputs to ‘reset’ the accumulated error in the grid pattern \cite{Fuhs:2006,Burak:2009,Pastoll:2013,Hardcastle:2015}. However, this ‘hard-resetting’ mechanism can lead to localization errors when sensory and path integration estimates mismatch and does not support efficient learning of these sensory associations in novel environments.

In the first part of this investigation, I ask whether principles of optimality based on the geometric properties of the grid cell firing pattern can explain the observed orientation offset and accompanying shearing with experience. Later, I develop these ideas in the context of continuous attractor models, a class of mechanistic models based shown to reproduce several characteristics of grid cells.
In the second part of this investigation I propose a novel, biologically plausible model of sensory integration in grid cells. The resulting system is capable of simultaneously navigating and learning sensory associations in novel environments and is shown to account for several unexplained experimental observations.

Next, I augment this system with the ability to perform offline inference of learned spatial associations. I propose that this inference is achieved by a process of message passing on a graph of learned locations (represented by place cells) and propose a novel biological mechanism. By allowing the system to schedule updates to learned locations based on the local convergence of the graph, I show that the process of offline inference generates sequences of reactivations which bear resemblance to the phenomenon of hippocampal replay.

Lastly, I conduct a novel analysis of local distortions to the grid pattern, relating the findings to theoretical work presented earlier in the thesis.
PUBLICATIONS


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IMPACT STATEMENT

Like any machine, animal brains need to encode and manipulate information about the world in order to successfully interact within it. Knowing one’s location and being able to reason about the structure of the world is paramount to this interaction. It is easy to take for granted the ease with which we as humans can manage this task. Even in today’s world, humans are in most cases far superior at performing cognitive tasks than their machine counterparts. In the words of Richard Feynman, “What I cannot create, I do not understand”. In designing machines to operate and think like ourselves, there is still much to learn about the way the brain solves real-world problems.

An important aspect of solving computational and cognitive problems is the nature of how the problem is represented. One cannot hope to make serious headway in cracking a problem if the relevant information is written on hundreds of unordered post-it notes. Rather, it is better to have them arranged with regards to some useful structure, such as their shared content or the place and time at which the note was made.

Place cells, found in the hippocampus, have been demonstrated to fire selectively in response to particular spatial locations or combinations of sensory input. Anatomically adjacent in the the medial entorhinal cortex are grid cells, which fire at multiple, hexagonally arranged locations in space. In contrast to place cells, which are thought to represent discrete locations in space, grid cells are thought to be an efficient way to relate these concepts to one another, allowing the brain to reason effectively and guide behaviour. Such a relationship might encode the spatial relationship between location A and B in physical space.

However, learning where to ‘store’ a concept in one’s ‘cognitive map’ requires the knowledge of where exactly you were when you experienced it. This problem is especially difficult when navigating for the first time in a new environment. One might consider seeing a post office along street A, when in fact you were walking along parallel street B. When you later passed that post office, you might mistakenly change your assumption about you current location from street B to A. Correcting these errors depends on reasoning about other contexts (you happen to live on street B and you know that there is no post office on your street).
My PhD work explored how the brain might solve these problems. Moreover, it examined how imperfections in doing so might lead us to build ‘warped’ impressions of space, which may be manifested in similar distortions of the firing properties of grid cells.

In addition to the goal of reverse-engineering aspects of brain function for the purpose of building our own, insights into these kinds of processing may help us to better understand how disease affects normal cognitive processing and provide means of developing early diagnoses. Alzheimer’s is known to develop in same anatomical region as grid cells and recent research suggests that studying spatial processing in healthy individuals might allow us one day to diagnose its onset before existing methods.
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MATHEMATICAL SYMBOLS

$A_{\text{min}}$ The minimum distance between one of the three grid axes and one of the walls

$X$ The size of the enclosing environment (m)

$\delta_{ij}$ Observed distance between landmark $i$ and $j$

$\lambda$ The distance between neighbouring peak in the firing rate map of the grid cell

$\phi$ The angle of the axis of the grid cell firing pattern relative to the x-axis (usually defined by the south wall)

$\sigma_{PI}$ Scalar describing the path integration noise

$u$ The velocity of the animal through real space

$x'$ A vector describing the position of the agent in physical space

$x$ A vector describing the position of the agent as represented on a hypothetical grid cell sheet

$z$ An observation in grid space

$d_{ij}$ True distance between landmark $i$ and $j$ as computed from their relative locations as stored in grid space

$u$ Presynaptic neuron firing

$v$ Postsynaptic neuron firing

$G$ Vector of grid cell firing rates

$P$ Vector of place cell firing rates

$c$ The vector spatial offsets of the grid cell firing pattern, in radians

$m$ Vector describing the location of a set of landmarks (place cells)

ellipticity The ratio between the semi-major ($r_a$ - longest dimension) and semi-minor ($r_b$ - shortest dimension) of an ellipse
ACRONYMS

BP  Belief propagation
BVC  Boundary vector cell
CAN  Continuous attractor network
CRT  Chinese Remainder Theorem
GC  Grid cell
HDC  Head direction cell
HF  Hippocampal formation
KF  Kalman filter
MA  Modulo arithmetic
mEC  Medial entorhinal cortex
OI  Oscillatory interference
PC  Place cell
PCA  Principal components analysis
PFD  Preferred firing direction
PI  Path integration
RBE  Recursive Bayesian estimation
RL  Reinforcement learning
sAC  Spatial autocorrelogram
SLAM  Simultaneous localization and mapping
SR  Successor representation
VCO  Velocity controlled oscillator
1. INTRODUCTION: THE COGNITIVE FUNCTION OF THE HIPPOCAMPAL FORMATION

Knowing ones location relative to the environment is crucial to the survival of most mobile creatures, and explicitly relies on environmental sensory input. Many organisms also use their own self-motion to maintain an estimate of location and orientation in the absence of sensory input, a process referred to as ‘spatial updating’ or PI (e.g., Mittelstaedt and Mittelstaedt (1980); for reviews see Etienne and Jeffery (2004); Barry and Burgess (2014)). Self-motion can be estimated from vestibular, proprioceptive and visual (e.g. optic flow) information and integrated over time to update an estimate of location (Etienne et al. (1996)). However, the cumulative nature of this PI process dictates that the underlying representations will also integrate error, making the estimate of location and orientation less reliable over time. These location and orientation estimates therefore need to be corrected by environmental sensory information whenever possible, rectifying any misalignment between the internally derived representation and the current perceptual estimate.

The HF contains several well described classes of neuron whose activity correlates with an animal’s location or orientation. These include PCs in the hippocampus proper, which fire in specific locations (O’Keefe and Dostrovsky (1971)); HDCs, found along Papez’s circuit, which signal the orientation of an animal’s head with respect to the environment (Ranck (1985); Taube et al. (1990a); Taube et al. (1990b)); GCs in the mEC, pre- and parasubiculum, which exhibit multiple firing fields arranged on a hexagonal grid (Hafting et al. (2005); Boccara et al. (2010)); and border or BVCs in the mEC and subiculum, which fire due to the presence of an extended boundary in a fixed allocentric direction (Barry et al. (2006); Savelli et al. (2008); Solstad et al. (2008); Lever et al. (2009a)).

In particular, the firing patterns of HDCs and GCs are thought to reflect the angular and translational components of PI, respectively (McNaughton et al. (2006); Taube
If this is the case, then these cells must receive both environmental and self-motion related sensory information, allowing them to update their activity according to PI and eliminate accumulated error according to perceptual information. Here, I consider both the functional implications of such a system on the grid firing pattern, and the practical implications of implementing such a system within the hippocampal circuitry.

### 1.1 Grid cells and path integration

GCs, which exhibit a unique hexagonal pattern of firing fields that tile a given environment, are thought to reflect the translational component of PI ([Hafting et al. (2005)](Hafting2005)). These grid patterns are characterized by their spatial scale (distance between grid fields) and orientation relative to the environment ([L.1A](#L1A)). Moving dorsoventrally along the mEC, GCs increase their scale in discrete steps ([Barry et al. (2007)](Barry2007); [Stensola et al. (2012)](Stensola2012); [Stensola et al. (2015)](Stensola2015)). GCs with similar scales share the same orientation relative to their environment but have offset firing fields, providing uniform spatial coverage ([Hafting et al. (2005)](Hafting2005); Fig. [L.1B](#L1B)).

In the rodent, GCs in layer II of mEC are likely comprised of both reelin positive stellate (or ocean) cells, which form the majority of principal neurons in mEC2 ([Gatome et al. (2010)](Gatome2010)), and calbindin positive (or island) pyramidal cells ([Domnisoru et al. (2013)](Domnisoru2013); [Kitamura et al. (2014)](Kitamura2014); [Ray et al. (2014)](Ray2014); [Sun et al. (2015)](Sun2015)). GCs have also been reported to exist with similar abundance in the pre- and para-subiculum ([Boccara et al. (2010)](Boccara2010)). However, unlike in layer II mEC, a significant proportion of GCs in these areas are strongly directionally modulated, similarly to those found in layers III, VI and VII ([Sargolini (2006)](Sargolini2006)). The co-existence of HDCs and BVCs in these areas not only suggests that these cell types are interdependent, but also raises the possibility that they might share similar mechanistic circuitry.

What evidence is there that the firing patterns of GCs reflect translational PI? Firstly, while PCs undergo re-mapping between different environments ([Muller and Kubie (1987a)](Muller1987a)), GCs preserve their firing patterns across all environments visited by the animal ([Hafting et al. (2005)](Hafting2005)). Importantly, the relative spatial offset of firing fields recorded from cells in the same module is also maintained across different environments ([Hafting et al. (2005)](Hafting2005); [Yoon et al. (2013)](Yoon2013); [Yoon et al. (2016)](Yoon2016)). These properties suggest that GCs whose firing fields share a similar scale and orientation form cohesive functional modules ([Stensola et al. (2012)](Stensola2012)). Moreover, in situations where the grids are unlikely to be directly driven by common environmental cues ([Barry et al. (2012)](Barry2012)), this invariance in spatial offset between grid firing fields within the same module also points to a shared PI mechanism ([Yoon et al. (2013)](Yoon2013)). Secondly, the spatial stability of grid firing fields decreases over time in darkness, in the supposed absence of corrective sensory inputs ([Hafting et al. (2005)](Hafting2005)), although
the rate of degradation is slower in mice (Pérez-Escobar et al. (2016); Chen et al. (2016)). Finally, lesion studies suggest that navigation tasks that rely specifically on PI mechanisms can be impaired after lesions of mEC (Van Cauter et al. (2013)).
Fig. 1.1: (A) Rotation of a black cue card causes rotation of the grid pattern. \( \phi \) shows the grid orientation, \( \lambda \) the grid scale (adapted from [Hafting et al. (2005)]). (B) Topologically neighboring GCs (red, green, blue) have different spatial phases, but equal scale and orientation (adapted from [Hafting et al. (2005)]). (C) Animals were placed in an environment with moveable walls (adapted from [Barry et al. (2007)]). GC firing patterns responded to uniaxial (top-right, bottom-left) and biaxial (bottom-right) contraction and returned to their original configuration (top-left). (D) Grids have three measures of orientation corresponding to their three axes. In a square environment, the angle from the wall is defined as the smallest of the three axis angles from their nearest wall. The smallest of these three angle clusters bi-modally about 7.5\(^\circ\) (adapted from [Stensola et al. (2015)]).

(E) Left: An example binned spike map in a 2.2 m\(^2\) box. Middle: Ellipses fitted to the innermost six peaks of the local autocorrelogram (different to right). Right: Ellipticity and gridness scores in different sections of a 2.2 m\(^2\) box, showing greater distortion near the edges (adapted from [Stensola et al. (2015)]). F Ellipticity and orientation can be corrected in some case by applying a shearing transformation (Stensola et al. (2015)). G Grid patterns in a 1D maze cannot be explained as cuts through a 2D hexagonal pattern (Derdikman et al. (2009)). H Grid patterns are distorted in non-hexagonal environments (Krupic et al. (2015)).

The fact that the location of GC firing fields are stable between visits to an environment, and that grid orientation rotates (along with the tuning curves of HDCs) with a prominent visual cue (Fig. 1.1 A; Hafting et al. (2005); Sargolini (2006)) indicates that GCs also receive environmental sensory inputs. More dramatically, reshaping a familiar rectangular environment along one axis can cause the parametric deformation of previously stable GC firing patterns along the same axis, resulting in both elliptical firing fields and grid patterns (Barry et al. (2007); Stensola et al. (2012), Fig. 1.1C). This suggests that, in familiar environments, sensory inputs can shift and deform the intrinsic metric generated by self-motion information. Interestingly, with repeated reshaping of the environment the expansion and contraction of GC firing patterns is diminished, suggesting that sensory inputs that are known to be unstable are eventually ignored mirroring similar results in HDCs (Knierim et al. (1995)).

How might environmental sensory inputs be used to correct drift in GC firing? Hebbian associations from PCs to GCs have been proposed as a likely route, given the convenient overlap between the PC firing fields and single nodes of a grid (O’Keefe and Burgess (2005)), with PCs mediating the effect of boundary manipulations via their proposed BVC inputs (Hartley et al. (2000)). However, it is equally possible that BVCs directly stabilize GC firing (Solstad et al. (2008)). Several theoretical studies have demonstrated that input from either PCs or BVCs is sufficient to ameliorate the effects of noisy self-motion input to the GC network (e.g. Fuhs and Touretzky (2006); Guanella et al. (2007a); Pastoll et al. (2013); Bush and Burgess (2014); Harcastle et al. (2015)). The spatial stability and parametric deformation of grid firing fields described above, for example, could be mediated by direct...
excitatory input from BVCs or PCs with firing fields either along the borders or distributed evenly throughout the environment, correcting the uniform hexagonal firing produced by self-motion inputs (Bush and Burgess (2014)).

Exploring the hypothesis that boundary input acts to stabilize PI, one study (Hardcastle et al. (2015)) analyzed the stability of GC firing patterns recorded in vivo with respect to rats encounters with boundaries. They showed that error in the grid fields (the mean distance between spikes and the center-of-mass of their nearest firing field measured across the whole recording session) increases with both time and distance since the last boundary encounter. Interestingly, both the magnitude and direction of the error was also consistent across all recorded GCs, suggesting a coherent drift of the grid pattern relative to the environment, as opposed to an increase in the size of individual grid fields. Moreover, error correction was greater in the direction perpendicular to the last boundary encounter, as might be expected if the grid were responding to BVCs that provide information about distance perpendicular to that boundary. These findings suggest that positional uncertainty may manifest itself as environmental misalignment of an intrinsically stable GC firing pattern, rather than a breakdown of GC firing patterns altogether. Furthermore, the hypothesis that GC firing patterns are stabilized by environmental boundaries predicts that time-averaged grid fields should be smaller and more elliptical near to the boundary, and that this effect would be more pronounced in larger environments.

Notwithstanding the possibility of direct boundary-related input to GCs, there is also evidence that input from PCs contributes to stable GC firing. For example, inactivation of the hippocampus rapidly disrupts the spatial periodicity of GC firing patterns, decreases the mean firing rate of GCs and increases their directional tuning (Bonnevie et al. (2013)). Moreover, stable PC, BVC and HDC firing patterns are known to precede stable GC firing patterns in the developmental timeline, suggesting that input from each of these cell types might be required for the generation of stable GC firing patterns (Langston et al. (2010); Wills et al. (2010)). Interestingly, it has recently been shown that the stability of PC firing fields is inversely correlated with distance to the nearest environmental boundary in pre-weanling rats, but that this relationship disappears in adult animals (Muessig et al. (2015)). This suggests that, prior to the development of GCs, inputs from BVCs active around the boundaries of an environment also serve to stabilize PC firing (O’Keefe and Neil Burgess (1996); Hartley et al. (2000)). Later in development, the appearance of stable place fields in the center of an environment coincides with the establishment of stable GC firing (Muessig et al. (2015)). However, whether PI input from GCs is required to stabilize place fields, or environmental sensory input from PCs is required to eliminate grid field drift away from environmental boundaries is yet to be determined.
1.1.1 Adaptation over multiple time-scales

The discussion so far has concerned interactions between place or boundary vector and GC populations according to pre-established neural connections. However, in new environments these connections must develop through synaptic plasticity over longer time-scales, and may be associated with gradual changes observed in GC firing patterns with increasing experience of an environment. Notably, the spatial scale of grid firing patterns reduces and their spatial regularity increases with experience of a novel environment (Barry et al. (2012)). At the same time, the orientation of the grid firing patterns relative to the boundaries of a square environment changes from an initially parallel alignment to develop a small (∼7.5 - 8.8°) angular offset (Stensola et al. (2015); Krupic et al. (2015); Fig. 1.1D). In larger square environments, local 7.5° orientation to multiple boundaries is observed, and is associated with a departure from the globally regular hexagonal firing pattern, resulting in local ellipticity (the skew of an ellipse tracing the innermost six peaks of a grid, see Fig. 1.1E).

In smaller square environments, both the angular offset of the grid firing pattern to local boundaries and its ellipticity can be modelled as a uniaxial shearing transformation - where grid fields are shifted away from one boundary by an amount proportional to location along that boundary - suggesting that both are the result of a common underlying process (Stensola et al. (2015); Fig. 1.1F). In larger square environments, the effects can be partially removed by applying a biaxial shearing centered about anchoring points in opposite corners. Whether or not the observed angular offsets and distortions of the grid fields that develop with experience, as well as the initial decrease in grid scale, serve to distort the perception of space or offer some functional advantage, are important questions that the following investigations will attempt to address. In either case, the influence of environmental boundaries on GC firing patterns seems likely to arise as a consequence of functional BVC inputs to GCs, possibly mediated by PCs (O’Keefe and Burgess (2005)), and which could counteract error accumulation (Hardcastle et al. (2015); Stensola et al. (2015)).

In addition to changes in GC firing patterns that may reflect their association to environmental sensory inputs, both PC and GC firing patterns are known to exhibit more gradual changes that reflect the slow disambiguation of perceptually similar environments. For example, on initial exposure to square and circular environments, place fields share preferred firing locations, measured relative to both a cue card and environmental boundaries, consistent with an important role of BVC inputs (Lever et al., 2002). However, over a period of days, firing locations in each environment diverge, either as a result of the gradual shifting of firing fields, or through the disappearance and emergence of the original and new fields, respectively.

Similarly, when rats are allowed to commute freely between two perceptually iden-
tical environments, GC firing patterns that are initially identical in both boxes gradually shift to form a unified, globally consistent representation with experience (Carpenter et al. (2015)). The alignment and spatial phase of the initially local GC firing patterns are consistent with conserved boundary-related inputs, and the subsequent shift suggests that, during navigation between the two environments, PI input slowly forces the sensory associations to be relearned. Interestingly, global (i.e. PI consistent) tuning of HDCs in connected environments emerges on similar timescales (Dudchenko and Zinyuk (2005)). Thus, longer-term adaptation may be important both in disambiguating perceptually similar environments, and in these localized representations within a consistent global framework.

1.1.2 Origins of sensory inputs to the spatial navigation system

The discussion to this point has considered how an effective spatial navigation system requires complementary information both from self-motion and environmental sensory inputs, and reviewed evidence that the firing patterns of HDCs and GCs reflect angular and translational PI, respectively, and receive the environmental sensory inputs needed to reduce errors in estimates of self-location that accumulate during PI. Thus, rather than representing pure PI, HDC and GC firing reflect the interface between self-motion and environmental sensory information. This distinction is particularly obvious in GCs, whose firing patterns are significantly more complex than required by the simple accumulation of displacement for translational PI, and provide a modular, high capacity code for location.

The basis of the cognitive map: place cells

Whereas GCs and HDCs are thought to be responsible for PI, PCs (O’Keefe and Dostrovsky (1971)) represent the current estimate of an animal’s location and, in combination with GCs, may support efficient navigation within a large-scale space (Fiete et al., 2008; Bush et al., 2015). Although PCs are downstream of the entorhinal cortex in what is considered to be a predominantly feed-forward processing circuit (Marr (1971)), PCs are likely to provide complementary input to GCs via projections directly to layers IV/V of mEC (Tamamaki and Nojyo (1995)).

PCs, typically pyramidal cells, exhibit high firing rates (5-15 Hz) in specific locations within an environment (their ‘place field’), with very low or zero firing rates elsewhere. However, even when an animal is located at a particular PC’s place field, firing is only observed during translational movement, which is associated with the 7-12 Hz hippocampal theta rhythm. Additionally, PCs exhibit phase precession, where during traversal of a place field, the firing of the associated PC occurs at successively earlier phases of the theta cycle, suggesting a dual temporal and rate code for location (O’Keefe and Recce (1993)). These combined observations have important implications for biophysical synaptic learning mechanisms (Markram et al.
(1997); Bi and Poo (1998); Mehta et al. (2002) which are known to be highly sensitive to spike timing on very short timescales. The compression of the relationship between successive PCs onto the timescale of single theta cycles has also influenced several theories of temporal order (Gupta et al. (2012)) and trajectory planning (Schmidt et al. (2010)).

Similar to GCs, PC field size also increases towards the ventral pole of the hippocampus (Jung et al. (1994); Kjelstrup et al. (2008)). In addition to the more obvious implications for the resolution of spatial encoding, the gradient in scale has also prompted speculation that episodic memories might be encoded in a similar manner (Poppenk et al. 2013), the 'richness' (Strange et al. (2014)) of an experience increasing towards the posterior (dorsal in rodents) pole in humans (Addis et al. (2004)). Additionally, only the ventral two-thirds of the hippocampus projects to the amygdala (Kishi et al. (2006)), suggesting that larger place fields may be more important for learning emotional associations with space, especially during fear-learning (Fanselow and LeDoux, 1999). There is some evidence to suggest that the place field width may be related to the 'richness' of sensory cues. In bats (Yartsev and Ulanovsky (2013)), fields were reported to be smaller when visual landmarks were present, however the question remains largely unaddressed.

PC fields are established quickly in novel environments (Jung and McNaughton (1993); Wilson and McNaughton (1993); Frank et al. (2004)) and remain stable between visits (Thompson and Best (1990)), though this association continues to develop over longer timescales. On a population level, PC representations of two perceptually different environments diverge (Lever et al. (2002b)). Individual PC firing fields also expand in size upon exposure to novel environments, similar to the scale expansion observed in GCs but on a faster time-scale, before eventually re-contracting (Barry et al. (2007)).

PCs have been mainly studied in CA1 and CA3 (O’Keefe and Dostrovsky (1971)) and to a lesser extent in CA2, although granule cells in dentate gyrus have also been found to exhibit multiple, smaller spatially tuned firing fields (Jung and McNaughton (1993)). The striking structural difference between the feed-forward and strongly recurrent network architectures of CA1 and CA3, respectively suggest distinct computational functions for the PC populations in each (Amaral and Witter (1989)), although existing experimental observations do not yet tell a consistent story. On a population level, the sparsity of representations differs significantly between subregions, the typical proportion of active cells ranging from 0.17-0.32 in CA3 and from 0.48-0.66 in CA1 (Leutgeb et al. (2004); Mizuseki et al. (2012)).

Additionally, although CA3 place fields stabilize more slowly (∼20 mins.) than in CA1 (∼3 mins), the representations generated are independent even for perceptually
similar environments, whereas those in CA1 show significant overlap, although these decorrelation processes both occur fast enough to develop over the course of a single trial (Leutgeb et al. (2004); Vazdarjanova and Guzowski (2004)). Although CA1 is downstream of CA3, the observation that both subregions develop independent representations over different timescales suggest that the former may develop directly from inputs from the entorhinal cortex (Brun et al. (2002)). The properties of individual PCs agree with these findings, CA3 place fields being more stable and carrying more information per spike than their CA1 counterparts (Mizuseki et al. (2012)).

The differences in representation between the two subregions can be reconciled with theories of pattern separation and pattern completion. In this context, pattern separation may be more effective in CA3 due to its dense recurrent connections, allowing the possibility of lower interference between independent 'attractor' states (Hopfield (1982); Amit (1989)). In contrast, pattern separation in PCs is represented by the phenomenon of remapping. Rate remapping refers to changes in the firing rate of PCs, predominantly in CA3 in response to minor changes in environmental features. With larger manipulations and changes of environment, global remapping occurs, with PCs adopting entirely new firing configurations and firing locations (Bostock et al. (1991); Anderson and Jeffery (2003); Leutgeb et al. (2005); Wills et al. (2005)).

**Integrating geometrical information: boundary vector cells**

The firing patterns of PCs in CA1 are robust to the lesioning of many different input streams, including CA3 (Brun et al. (2002)), mEC (Miller and Best (1980); Brun et al. (2008)), lEC (Lu et al. (2013)), pre- and para- subiculum (Liu et al. (2004)), and subcortical structures (Miller and Best (1980)). Thus, it seems likely that PC firing patterns are supported by a wide range of multi-modal inputs that converge on the hippocampus from a variety of different cortical structures. Accordingly, PC firing fields are modulated by contextual inputs such as wall color and odor (Bostock et al. (1991); Anderson and Jeffery (2003); Lu et al. (2013)), manifested in PC remapping. Although these types of information are clearly important to the formation and stability of PC firing fields, it is not clear how they would explain the responses of PCs and GCs to manipulations in the geometry of an environment.

Importantly, it has been hypothesized that BVCs are a potential source for the environmental determination of the spatial firing locations of PCs. Several theories have addressed the problem of mapping boundary related inputs to form place fields (Zipser (1986); Sharp (1991); Burgess et al. (1994); O’Keefe and Neil Burgess (1996)), though recent models have focused on the specific inputs from BVCs (Hartley et al. (2000); Barry et al. (2006); Barry and Burgess (2007)), the latter also extending earlier work to incorporate the experience-dependent plasticity in the
BVC-PC wiring.

The BVC model of PC firing makes a number of predictions, many of which have since been experimentally validated. Principal among these were the discoveries of boundary cells in mEC (Savelli et al. (2008); Solstad et al. (2008)) and BVCs in subiculum (Lever et al. (2009a)). Whereas boundary cells fire exclusively near boundaries, BVCs fire due to the presence of an extended boundary in a fixed allocentric direction, which may lie away from the boundary. The firing fields of these BVCs become broader with increasing distance from the animal, presumably reflecting the increase in uncertainty according to visual input.

These models successfully explain observations that uniaxial stretching of a familiar rectangular environment cause similar stretching of place fields (O’Keefe and Neil Burgess (1996)). Since PCs are theorized to arise from the thresholded sum of a population response, the model also predicts that PCs should respond to specific geometric configurations of environmental boundaries. As predicted, PCs develop secondary firing fields in response to barriers introduced to familiar environments (Hartley et al. (2000)). Extensions introducing plasticity into the model (Barry and Burgess (2007)) successfully describe the later disappearance of one of the two firing fields (Lever et al. (2002a); Rivard et al. (2004); Barry et al. (2006)).

Additionally, the existence of boundary cells in mEC suggests an input to GCs. While no direct projections have been established from the subiculum to mEC, there is reciprocal connectivity between subiculum and CA1, providing a possible anatomical grounding to the theory.

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Egocentric to allocentric representations: head direction cells

Although the roles of GCs and HDCs in performing translational and angular PI have so far been considered as independent streams, the translational component in fact relies on a directional reference. Additionally, it is important to note that BVC firing patterns are allocentric representations, their firing depending only on the animal’s location, independent of its head direction.

By contrast, sensory representations are necessarily egocentric in nature. Hence, environmental sensory inputs to BVCs will at some stage require an egocentric-allocentric coordinate transformation. One such mechanism for transformation between population codes in different frames of reference has been proposed, involving an expanded gain field representation formed by the product of both individual sets of basis functions (Salinas and Abbott (1996); Pouget and Sejnowski (1996); Burgess et al. (2001); Byrne et al. (2007)). To account for the allocentric firing patterns of BVCs, it has been hypothesized that BVCs in the HF have an egocentric analog in medial parietal areas (Burgess et al. (2001); Byrne et al. (2007)). These putative cells would signal the presence of boundaries at given distances in an egocentric
frame of reference via receptive fields in peripersonal space. This egocentric representation could be driven directly by sensory input and transformed to an allocentric representation via a gain field circuit in posterior parietal or retrosplenial cortex. This egocentric-allocentric transformation depends on the head direction system to correctly map egocentric into allocentric direction (e.g. North corresponds to left when facing East).

This directional reference is proposed to be supplied by HDCs, whose PFDs exhibit a Gaussian tuning curve centered around the animal’s facing direction relative to its environment. Similarly to GCs, HDCs are thought to maintain this estimate of facing via a combination of angular integration of vestibular information (the angular analogy to PI) and reference to environmental cues [Stackman and Taube].
Unlike GCs, HDCs are weakly boundary-dependent and are instead much more sensitive to distal landmarks, which are more stable in the visual field (Taube et al. (1990b); Jeffery (1998); Zugaro et al. (2001); Clark et al. (2012)). Retrosplenial cortex and postsubiculum are thought to be the main gateway to this visual information (Taube (2007); Vann et al. (2009)).

Similarly to GCs, HDCs are also able to maintain an estimate of their PFDs in absence of sensory cues. However, drift is observed over time, consistent with the noisy accumulation of error (Taube et al. (1990b); Mizumori and Williams (1993); Goodridge et al. (1998)). PFDs are also conserved between visits to the same environments, hinting at robust internal circuitry (Taube et al. (1990b)), possibly mediated by attractor dynamics (Peyrache et al. (2015); Seelig and Jayaraman (2015); Green et al. (2017)).

HDC representations can also be deliberately manipulated. Shifting a salient landmark between visits to the same environment causes the PFDs to shift equivalently (Taube et al. (1990a) and Taube et al. (1990a)). This shifting also occurs in the presence of the animal, though a slight lag is observed suggesting that a fast-action plasticity mechanism is responsible for updating the new representations based on the previously learned values (Knight et al. (2013)). Interestingly, the relationship between all HDCs’ PFDs is conserved, suggesting that the generative circuitry is linked and further supporting the analogy to GCs. Furthermore, drifts in PFD correlate with angular error in homing tasks, implying a direct role in cognitive function (Valerio and Taube (2012)).

Unlike GCs, HDCs are found widely throughout the HF. Although lesion studies suggest that the generative circuitry is likely to reside largely upstream in the dorsal tegmental nucleus and mamillary bodies (Blair et al. (1998); Bassett et al. (2007)), HDCs are in fact found throughout Papez’s circuit, including the anterior and lateral dorsal thalamus, dorsal presubiculum, in addition to mEC (Sargolini (2006)) and retrosplenial cortex (Chen et al. (1994)).

Thus, boundary-related input would arrive at the HF from the dorsal processing stream (Goodale and Milner (1992); Mishkin and Ungerleider (1982)) via the parietal, retrosplenial, parahippocampal and medial entorhinal cortices. By contrast, contextual and object-related inputs (Deshmukh and Knierim (2011); Lu et al. (2013); Tsao et al. (2013)) likely arrive from the ventral processing stream via perirhinal and lateral entorhinal cortices. Hence, these pathways carry complementary sensory signals (see color code in Fig. 1.2), which provide input to PCs and GCs independently, increasing the robustness of the global path-integration system.
1.1.3 A coherent interdependent network for spatial processing

The discussion to this point has focused primarily on unidirectional processing pathways, i.e. the transmission of environmental information directly to HDCs, or via BVCs and PCs to GCs. However, it is important to note that GCs are also likely to project to PCs in the hippocampus (van Strien et al. (2009)), and it has been suggested that GCs can partially support and update PC firing when sensory inputs are reduced (e.g. in darkness). Accordingly, evidence indicates that when visual and PI information are dissociated, the resulting PC firing is best described by a balanced combination of these inputs (Gothard et al. (1996); Chen et al. (2013)).

More generally, it makes sense that our perception of spatial location and orientation combines both types of input. Behavioural evidence in humans further suggests that the two input streams are integrated into a single representation (Tcheang et al., 2012), and are possibly weighted to reflect the relative reliability of the available sources of information (Nardini et al., 2008). Thus, reciprocal connectivity between PCs and GCs is likely to underlie the concurrent development of stable PC and GC firing fields away from the boundaries of an environment (Muessig et al. (2015)), in order to form a single multimodal representation of location. Similarly, HDC input is critical for the transformation of egocentric sensory input to allocentric BVC and PC firing patterns, all of which rotate coherently with HDC firing patterns when a single prominent cue is shifted in a circular arena (OKeefe and Conway, 1978; Muller and Kubie (1987a); Knierim et al. (1995); Sargolini (2006)). Conversely, spatial information from PCs and GCs is likely involved in the development of coherent HD representations across connected environments (Dudchenko and Zinyuk (2005); Bicanski and Burgess (2016)). To summarize, these data suggest that the different spatial representations found in and around the hippocampal formation are mutually interdependent and support a coherent unitary representation of space based on both environmental sensory and PI inputs.

1.2 Models of grid cell firing

There is a rich history of theoretical modelling in the GC field, many of the original models drawing inspiration from previous work on PCs. Since their discovery, elucidating the mechanism underlying the generation of GCs has fuelled a fierce debate that has driven advancements both in theoretical and experimental techniques. Indeed, the fascinating narrative that has unfolded is in many ways an excellent example of the productive theory / experiment symbiosis that should in principle be the backbone of all scientific endeavours.

Of the numerous models that have been proposed to explain the spatial firing of GCs, the earliest and most numerous rely on the assumption that the velocity of the animal in two or more component directions is integrated over time and used to update
an internal state encoding location. This ‘path integrator’ class of models have traditionally taken a mechanistic view, prompting detailed anatomical predictions. This class includes oscillatory interference (Burgess et al. (2007)) models, continuous attractors (Fuhs and Touretzky (2006); McNaughton et al. (2006)) and others.

In contrast, recent models of GCs tend to ask not ‘how’, but ‘why’? This ‘functional’ class of models are either agnostic to the underlying mechanism and simply consider the function of the resulting grid patterns (Fiete et al. (2008a); Mathis et al. (2012)) or assume that GCs are formed exclusively from sensory inputs and perform a higher level function independent of PI (Dordek et al. (2015a); Stachenfeld et al. (2017)).

1.2.1 Mechanistic models of PI

The path integrator class of models can be broadly divided into two main subclasses. OI models encode location as a phase difference between two or more oscillators, whereas CAN models encode location explicitly as the location on a cyclic phase-space (an ‘attractor plane’), which can also be interpreted as a phase. These phase spaces are typically represented biologically by networks of neurons which can, by virtue of their connectivity, maintain a stable population firing pattern. However, this dichotomy is somewhat misleading when considering some models (Blair et al. (2007); Blair et al. (2008); Mhatre et al. (2012); Schmidt-Hieber and Husser (2013); Bush and Burgess (2014)) which incorporate elements of both. Instead, these models can be better differentiated in terms of how they achieve three principal sub-goals which are crucial to the functioning of a biologically plausible GC mechanism, namely:

1. How is position encoded within the model?
2. How is this position updated?
3. How is this position, encoded internally, read out to produce a hexagonal firing pattern?

However, these three requirements only define the desired function of the system, corresponding to the first (computational) stage of Marr’s (Marr and Poggio (1977)) framework for information systems. A complete GC model would need to implement these functions in a biologically plausible way, which introduces two additional constraints:

4. How do the synaptic weights in the system self-organise?
5. How would the animal incorporate information from its environment to stabilize the grid pattern?

Of these five requirements, the first provides the closest analogy to the broad OI vs. CAN classification (Zilli (2012)). 1D coding mechanisms, corresponding broadly to
OI models, encode linear distance in two or more directions in independent mechanisms, combining them in the readout stage to produce a 2D representation of location. In contrast, other models represent the 2D location explicitly, broadly describing the mechanism of CANs. In these latter models, the ‘readout’ mechanism is obtained simply by the cells on the attractor sheet firing according to the bump activity, which tracks the animal of the animal.

![Mechanistic models of grid cell firing](Fig. 1.3: Mechanistic models of grid cell firing)

**1D encoding**

As discussed, a distance in 1D can be represented in a number of ways. The most obvious candidate might be to encode this value in the firing rate of single neurons (Gaussier et al. (2007); Hasselmo and Brandon (2008)), a mechanism known to be employed by oculomotor neurons in the encoding the horizontal angle of gaze in invertebrates (Lopez-Barneo et al. (1982)). However, the value encoded within these rate-proportional codes will be limited by the firing-rate range of each neuron. Given that GCs encode phase, as opposed to distance, this constraint does not preclude the possibility of the use of such a mechanism, as the phases are by definition constrained to take values within a predefined range. However, given the irregularity of individual neuronal spiking, accurate rate-based codes rely on the average of a large population of neurons, which can be inefficient. Secondly, the response of the firing-rate must be linear over the range of values to be encoded. Lastly, the energetic cost of maintaining each value would be different according to the firing-rate. Though these issues could in principle be addressed by the network architecture, the periodic nature of GC encoding has led most modelling attempts to employ similarly periodic mechanisms of encoding these scalar values.

An alternative method of encoding phase within a predefined distance range is to use ring attractors (Ben-Yishai et al. (1995); Zhang (1996)), which encode phase...
as a stable ‘bump’ of persistent activity. The activity bump arises spontaneously from a specific connectivity scheme whereby cells adjacent in the ring are mutually excitatory, whereas cells further apart are inhibitory. Unlike discrete attractors, the bump can occupy any continuous-values position along the ring, though the representation is increasingly subject to noise as the number of cells in the ring decreases. Ring attractors have been found to encode orientation tuning in visual cortex (Ben-Yishai et al. (1995)) and more recently head direction in flies (Seelig and Jayaraman (2015); Green et al. (2017)). The latter discovery is particularly interesting for similar models of GC firing, considering the proximity and similar function of HDCs and GCs in the HF.

Without external input the activity bump will theoretically remain stationary, although in reality their location is subject to random drift over time. However, their position can be modulated by external input, causing the position of the activity bump to shift. In the case of a constant translatory input, the bump will oscillate around the ring at a fixed frequency. The latter forms are termed ‘biased’ ring attractors (Eliasmith (2005)) or ‘ring oscillators’ (Blair et al. (1998); Welday et al. (2011); Blair et al. (2014); Bush and Burgess (2014)), as opposed to the former ‘unbiased’ forms which maintain a stationary bump.

Other approaches use the inherent periodicity of LFP rhythms, notably in the 6-10 Hz Theta range (Burgess et al. (2007); Giocomo et al. (2007)) to encode phase information. Later models have made efforts to transpose the mechanisms on to spiking dynamics (Burgess (2008); Hasselmo and Brandon (2008); Zilli and Hasselmo (2010)).

2D encoding

In contrast with 1D encoding schemes, CAN models explicitly encode the position of the animal in real-space as the position of an activity bump on a 2D ‘attractor-sheet’ (Zhang (1996); Samsonovich and McNaughton (1997); Fuhs and Touretzky (2006); Guanella et al. (2007a)), the direct 2D analogy of a ring attractor. It is here that the distinction between OI and CAN models first breaks down, since some OI models also incorporate CAN dynamics.

The simplest and most commonly used form of a 2D attractor in the GC literature considers a square or rectangular plane which, if folded in 3D with its opposing edges connected would form a torus. However, although a single bump of activity can be moved continuously about the surface of this torus to track the \(xy\) movement of an animal in real-space, the resulting firing, when plotted against position, corresponds to a square rather than hexagonal grid pattern. To solve this problem, the plane can be connected to form a ‘twisted torus’ (Guanella et al. (2007a)). Here, the right and left sides are connected as before (forming a cylinder), however the top right half
Fig. 1.4: ‘Twisted-torus’ connectivity in continuous attractor network models generates hexagonal grid cell firing patterns. The grid cell sheet (a single ‘module’; Hafting et al. (2005)) can be represented as a rhombic tile (A), or a twisted-torus in 3D (B). The grid cell module can be tiled across physical space (C; here, a birds eye view of a square box), such that the activity of a single cell (red) will be periodic when mapped in space. This is the firing rate map of the grid cell. D shows the experimentally observed equivalent. Adapted from Bush et al. (2015).

is connected to the bottom-left half (the cylinder is twisted by half a turn before connecting the ends). Alternatively, the velocity inputs which drive the movement of the bump can be modulated along one axis, although this implementation produces elliptical, rather than circular grids (Zilli (2012)).

Attractor planes with simple torus connectivity can also support multiple activity bumps, which when pre-established in a hexagonal pattern remove the necessity for the more complex twisted-torus connectivity (McNaughton et al. (2006); Fuhs and Touretzky (2006); Burak and Fiete (2009); Couey et al. (2013)). However, the main problem with these models is that they require the scale of the grid pattern to be compatible with the scale of the attractor plane to be fully periodic (for the pattern to ‘tile’). This problem is discussed in more detail in chapter 3.

By shifting multiple rather than a single bump, periodicity in the firing of individual cells on the sheet is inherently built in to the model. By continuously monitoring a single cell (for example, the central cell) in the attractor sheet, moving the grid pattern will cause the cell to fire at some locations, but not others. Thus, the only function of the periodic boundary conditions is to allow the pattern to be shifted continuously. However, another way of achieving this is by simply tapering the connection strengths or firing rates to zero at the edges of the attractor sheet (Fuhs and Touretzky (2006); Burak and Fiete, 2009). In these ‘aperiodic’ networks, grid fields ‘fade out’ as they are moved towards the edges and are replaced by another field ‘fading in’ at the opposite edge. The principal advantage of these arrangements is that they are able to support arbitrarily sized grid patterns.

Oscillatory interference models

OI models encode location as the phase difference between two or more oscillators. Since an oscillator’s frequency $\omega$ is simply the rate of change of its phase $\phi$, $\omega = \frac{d\phi}{dt}$,
the derivative of the phase difference is just the difference in the frequencies:

\[
\frac{d}{dt}(\phi_1 - \phi_2) = \frac{d\phi_1}{dt} - \frac{d\phi_2}{dt} = \omega_1 - \omega_2
\]

Since the difference in frequencies is proportional to the animal's speed, the phase (which is the integral of the frequency difference) will represent the phase, or distance travelled in the velocity controlled oscillator’s (VCO) preferred direction. Biologically, the 'readout' is achieved by neuronal spiking that is produced by the thresholded sum of two interfering oscillations in the cell membrane, one of which is usually taken as the globally constant theta oscillation and the other a cell-specific VCO. The frequency of the VCO is modulated by the projection of the animal’s running direction onto a preferred firing direction. Interference between the and the global theta oscillation produces periodic bands of activity in the VCO’s preferred direction. Hexagonal firing patterns can be generated through the interference of multiple periodic bands spaced at 60° intervals (Burgess et al. (2007); Giocomo et al. (2007)). In these early models, the input from three VCOs are summed in the dendrites of a single GC. Later models (Burgess (2008); Zilli and Hasselmo (2010)) encode the distances in each direction in independent modules, which are combined in the downstream GC, recognising that multiple oscillators would likely phase-lock if present in the same cell (Remme et al. (2010)).

OI models successfully explain phase precession in PCs (O’Keefe and Recce, 1993) and GCs (Hafting et al., 2008), which has yet to be addressed in CAN models in more than one dimension (Navratilova et al. (2012)). However, GCs have been observed even when theta is abolished (Giocomo et al., 2009) and in fruit bats and macaques (Yartsev et al. (2011); Killian et al. (2012); Heys et al. (2013)) where the theta rhythm is intermittent or not present. However, OI models operate equally well with any frequency of baseline oscillation, which need not be constant over time since the location is encoded in the phase difference between two oscillators (Burgess, 2008; Blair et al., 2012; Orchard et al., 2015).

Another criticism of OI models is that the regular separation of the VCO inputs must be preconfigured, although it has been suggested that this could arise through a Hebbian learning mechanism (Burgess et al. (2007); Mhatre et al. (2012)).

Continuous attractor models

The hexagonal pattern in CAN models is, as in the single bump case, maintained and established by virtue of symmetric recurrent connections between cells on the attractor plane (Fuhs and Touretzky (2006); McNaughton et al. (2006); Guanella et al. (2007a); Burak and Fiete (2009)). Although there is subtle variation in the connectivity profiles among models, all share the two basic properties where cells
that are proximal on the sheet are mutually excitatory whereas cells further away are inhibitory. However, unlike in a typical single-bump connectivity scheme, the inhibition reduces to zero at a fixed distance, allowing multiple bumps to form at regular intervals. In these ‘circular-surround’ schemes, the hexagonal patterns that emerge spontaneously and stably can be related to the analogous problem of optimal circle-packing (Shannon (1948); Conway and Sloane (2013)). This argument has been extended to posit the likely form of GC firing patterns in 3D (Mathis et al. (2015)).

The classical form of this connectivity profile is often referred to as a ‘Mexican-hat’ (Amari (1977a)), though a square-wave scheme (Couey et al. (2013)) has also been demonstrated to reliably produce hexagonal firing. Indeed, the mexican-hat profile can be generated in a number of ways, including as a decaying cosine wave or difference of Gaussians (see chapter 3 and Fig. 1.5). However, although mexican-hat profiles are known to exist in other areas, notably visual cortex (Kang et al. (2003)), experimental evidence suggests that no recurrent excitatory connections exist between LII mEC stellate cells, which instead are thought to interact exclusively via inhibitory interneurons (Dhillon and Jones (2000); Couey et al. (2013); Pastoll et al. (2013)).

Despite this finding, theoretical studies have shown that stable GC firing patterns can be generated in recurrent inhibitory networks (Couey et al. (2013)) and in networks with two distinct subpopulations, corresponding to interneurons and pyramidal cells (Pastoll et al. (2013)). The latter model also demonstrated that theta-nested, gamma oscillations can emerge within the same network. These ‘clock-like’ oscillations may act as a temporal reference signal, enabling coincidence detection by downstream neurons in dentate gyrus (Buzski et al. (2012)) or allowing distinct cycle-specific encoding of information (Lisman et al. (2005)).

However, these models all rely on the assumption of a global excitatory input to the mEC cells, which effectively shifts the purely inhibitory weight profile to achieve a
net local excitation (Couey et al. (2013); Fig. 1.5c). No strong candidate for this excitation has been established, although the hippocampus has strong projections to superficial layers of mEC (van Haeften et al. (2003); Kloosterman et al. (2003)), a finding supported by the observation that GC firing is abolished in absence of these projections (Bonnevie et al. (2013)). Alternatively, GCs are also abolished in absence of medial septum input (Brandon et al. (2011); Koenig et al. (2011); Winter et al. (2015)), another possible source of this excitatory input.

In a putative CAN, cells that are more proximal on the attractor sheet should be preferentially connected. However, this is a difficult hypothesis to explore due to the lack of topographic relationship to their positions in real-space. However, cells that are more proximal on the attractor sheet, according to the grid pattern, should have more similar phases, an experimentally more tractable statement of the problem. Despite this, no studies have been able to clearly establish whether or not GCs with similar spatial phases are preferentially connected, a matter further complicated by the likelihood that GCs are connected disynaptically via interneurons. One study showed that the rate maps of pairs of GCs projecting to the same interneuron were no more similar than chance (Buetfering et al. (2014)), though it is unclear whether the correlation between random pairs of GCs may be be higher than would be expected if they were indeed independent, reflecting the possibility that all pairs receive similar but temporally shifted inputs. In contrast, a number of studies have found that noise correlations decreased with increasing difference in spatial phase (Mathis et al. (2015); Dunn et al. (2015); Tocker et al. (2015)), however it is not possible to determine from correlational analysis whether these connections are excitatory or inhibitory, due to common inputs or local network synchrony.

As in the case of OI models, it is not clear how these putative connectivity patterns might be learned, a matter again complicated by the fact that the connections are not necessarily topographic in the brain. A recent study (Widloski and Fiete (2014a)) addressed this in part, showing that the weights could theoretically be learned via STDP. Interestingly, by assigning random directional tuning the learned weights are asymmetric, allowing the resulting network to perform PI (Sargolini (2006); Burak and Fiete (2009)). However, their model relies on the assumption that the GCs receive location-specific inputs, as might be provided by PCs. Essentially, the GC connections then develop based on the correlation in firing between their respective inputs. Another recent study (Dordek et al. (2015b)) showed that the weights in a PC-GC network, when learned using PCA (Oja (1982a)) produce a grid-like firing pattern when projected back onto the PC inputs. In their neural network implementation, successive principal components are learned by subtracting the projection of the previous principal components in a Gram-Schmidt orthogonalization procedure. However, it is also possible to implement inhibitory connections
between the GCs, allowing all principal components to be learned simultaneously (Földiak (1990)). Since the GC firing is inhibitory, the GC patterns learned are spatially non-overlapping, suggesting a possible mechanism for ensuring this trait as found in multiple GC modules. It is possible that by allowing the GC-GC weights to be learned, more realistic mexican-hat like connectivity could be learned, although hard-wired inhibitory connections could also be considered more akin to the square-wave connectivity shown to also produce grid patterns (Couey et al. (2013)).

Multiple mechanisms have been suggested for the means by which GC firing patterns might track the movement of the animal, but all involve spatially asymmetric network interactions modulated by the animals direction and speed of movement, analogous to those proposed for head-direction circuits (Skaggs et al. (1995); Zhang (1996)). These asymmetries, which may be mediated by directional or conjunctive GCs (Fuhs and Touretzky (2006); McNaughton et al. (2006); Sargolini (2006)) and by speed cells (O’Keefe et al. (1998); Sharp and Turner-Williams (2005); Sharp et al. (2006); Kropff et al. (2015a)), generate depolarization in GCs whose firing fields lie along the movement trajectory adjacent to the current location, causing a shift of the grid firing pattern in that direction. Irrespective of the specific mechanism, translation of GC activity patterns according to self-motion information requires accurate heading information and, accordingly, it has been demonstrated that inactivation of HDCs in the anterior thalamic nuclei also leads to a loss of periodic grid field firing (Winter et al., 2015a). In contrast, conjunctive cells, unlike GCs do not exhibit phase precession, which might be expected if they were directly driving GC firing (Climer et al. (2013)), a question that can also be asked of the lack of phase precession in inhibitory interneurons (Bush and Burgess (2014)). More generally, preliminary results have found little evidence of the strong temporal correlations that might be expected between conjunctive cells and GCs (Tocker et al. (2015)).

How is error-resetting according to environmental inputs implemented in a CAN? A crucial component of a CAN network that performs accurate PI is that the stable activity pattern be translation invariant. However, this requires that the connectivity patterns described earlier be completely symmetric, possibly a difficult ask of a biological network (Zhang (1996); Battaglia and Treves (1998)). Asymmetries lead to an uneven or ‘sticky’ attractor landscape, where certain locations will act as basins of attraction for surrounding locations such that an activity bump is forced to settle in discrete locations when tracking a continuous location in real-space. This scenario quickly leads to noise accumulation and drift away from the correct estimate of location.

Clearly, some error-correcting input is required from the environment to prevent drift in the putative, biological system and indeed in idealised simulations (chapter 3). To date, most models rely on preconfigured connections between either PCs or
boundary cells (not BVCs) and GCs to intermittently provide resetting input to the GC representation (Burak and Fiete (2009); Couey et al. (2013); Pastoll et al. (2013); Hardcastle et al. (2015)), a mechanism that is unsatisfactory for two principal reasons. Firstly, the resetting according to PC inputs relies on the correct location at that instant being known, eliminating the purpose of performing PI. Secondly, there are challenging questions regarding the learning of these associations in novel environments.

1.2.2 Functional perspectives

Whereas the discussion in the previous section considered the 'how' underlying the generation of GC firing patterns, the burning question still remains as to why the entorhinal cortex should represent non-periodic (linear) space as a set of periodic (cyclic) sub-spaces which vary in scale along the dorso-ventral axis of the mEC. Although GCs within a module appear to be behave coherently, GCs from different modules which may or may not possess differing intrinsic scales, orient themselves differently in response to the same environmental features. This is a challenging question to the parsimonious theory that modules of different scales operate as an interdependent hierarchy.

These questions are extremely difficult to address concretely via experiment. It is perhaps for this reason, in addition to the broad connectivity of the hippocampal formation that has led to speculation over the role of the entorhinal cortex beyond performing PI. These theories will be expanded upon in the following section, but can be broadly divided into decoding and encoding models. As will be discussed, the simplistic distinction between ‘mechanistic’ and ‘functional’ becomes fuzzy; several of the models described provide insights into both.

Hierarchical location decoding

Given a population of GCs, whose firing may be be dictated by any of the aforementioned mechanisms and whose firing patterns vary in spatial scale and orientation relative to environmental landmarks, what might then be the use of such a representation? One might intuitively assume that the PC code which unambiguously codes for spatial locations would be more attractive than a single GC’s, which fires when the animal is near any of the vertices of the hexagonal lattice. Theoretical analyses have nonetheless uncovered interesting properties of these called 'modulo' codes (Gorchetchnikov and Grossberg (2007); Fiete et al. (2008b)).

In devising the coding scheme there are several properties that may be varied, notably the number of cells in each module, the number of modules and the scales of those modules. In nested coding schemes, the current location is decoded in a top-down fashion, successively refining the precision of the estimate by reading out
the phases of modules with successively smaller grid scales. A drawback of such schemes is that the maximum decodable range is limited by the largest grid scale.

Analyses have typically focused on the capacity of a given encoding scheme, defined as the maximum spatial range within which the location can be decoded with a fixed resolution. In the context of abstract binarized (ON/OFF) GCs, this becomes the maximum spatial range within which each combination of phase values corresponds to a unique decoded location (Bush et al. (2015)). There is therefore an inherent trade-off between range and resolution. Analysing nested codes, Wei et al. (Wei et al. (2013)) found that the capacity could be optimised by setting the largest grid scale to the maximum coding range, then optimizing the resolution by setting the remaining scales such that each successive scale is a common multiplicative factor smaller than the previous (i.e. defining a geometric progression). Moreover, the optimal factor was found to be equal to $\sqrt{e} \approx 1.65$, matching empirical observations.

However, if not optimizing for a specific range the grid code could theoretically represent distances much larger than the largest grid scale by using a MA scheme. In MA codes the grid scales must be slightly different, but there is no requirement for the range of scales needed in nested codes. Rather, the choice of grid scales is motivated by reducing ambiguity between modules. The CRT states that the maximum range of an integer modulo code is equal to the lower common multiple (LCM) of the scales. If the modules scale with an integer factor, a module with a scale $\lambda = \frac{1}{2}$ would intersect with another module with scale $\lambda = 1$ twice per single revolution of the latter; i.e. the lowest common multiple is equal to the largest grid scale. However, if the ratio of scales is coprime (e.g. $\lambda = 3, 5$), the LCM is greater than the largest grid scale, theoretically allowing the system to decode up to the product of the grid scales (Gorchetchnikov and Grossberg (2007)).

Fiete et al. (Fiete et al. (2008b)) extended the results of the CRT to arbitrary non-integer grid scales. The authors demonstrate that the capacity of a MA GC code is a more efficient representation than that of PCs; fewer cells are needed to represent a specific range and resolution. Moreover, the maximum encodable range is much greater than the largest grid scale. This is an important requirement if the grid code is to be of utility to the animal; the largest grid scale measured to date is on the order of metres in rats, which forage over distances up to 1km in the wild (Recht (1988))

Results obtained from analyse based on optimality should however be taken with

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Footnote:

1 It is possible that the current observed range and canonical form of grids cells is in part an ethological phenomenon, reflecting the typical environment that laboratory animals are exposed to. Preliminary results from the laboratory of Prof. Noam Ulanovsky conducted in freely roaming bats with wireless ePhys units show PCs with fields much larger than have been previously reported. It is not unlikely that GCs with larger scales may be observed in this context, although GC firing patterns appear to be less stable or non-existent in 3D space.
a pinch of salt. Towse et al. (Towse et al. (2014)) analyzed both MA and nested codes in the presence of neuronal noise, finding that co-prime and non-integer factor set scales performed equally well. Advancing this argument, Vago et al. (Vágó and Ujfalussy (2018)) suggested that when the coding accuracy of the system is limited by neuronal noise, the strict requirements on choices of grid scale disappear completely. Indeed, the authors demonstrate that the system approaches optimal capacity when the grid scales are randomly chosen.

Results from the previous analyses are based on the assumption of a base set of grid modules, whose cells exhibit hexagonally tiled firing pattern across space. But why hexagons? Mathis et al. (Mathis et al. (2015)) analyzed arbitrary periodic lattices in terms of their decoding resolution, defined as the accuracy with which an ideal observer can deduce the encoded location given the firing of the GC population. The resolution is shown to be related to the Fisher information, an information theoretic measure that is maximized for hexagonal lattices and is optimized under the assumption of maximum-likelihood decoding. More intuitively, the result is related to the packing density, which is the density with which the lattice is able to cover space.²

Vector navigation using GCs

A characteristic trait of animal navigation is the ability to navigate directly to goal locations (O’Keefe and Conway (1978)) without relying on the repetition of a previously learned trajectory (Packard and McGaugh (1996)) or following explicit sensory cues (Morris et al. (1982)). As demonstrated by Tolman, the path taken to a novel or previously visited location may even utilize ‘shortcuts’ which take routes through parts of the environment that have not previously been visited by the animal (Tolman (1948)). It is thought that this ability may be underlined by a mechanism for computing a ‘vector’ path (a direction with magnitude) from one location to another, which would in the first instance require a neural representation of the two locations which also reflected their relative locations in real space.

Again, PCs immediately spring to mind as a suitable candidate for performing these vector calculations. A simple way to navigate towards a goal might be to compare the representations of the current and desired location and move so as to increase their similarity (Burgess and O’Keefe (1996)). However, this method would be limited to the width of the largest place fields unless combined with experience-dependent learning, which could allow the chain of PCs between the two locations to sequentially activate a previously experience path (Blum and Abbott (1996)), although this method would not represent a direct ‘vector navigation’ solution, in-

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² The same analysis also predicts that in 3D, GCs should adopt a face-centered cubic configuration where a sphere in the next layer in the z-direction is located at the midpoint of the triangle formed by three spheres in the layer below in the x-y plane.
stead being biased towards previously learned trajectories which may themselves be suboptimal. It is theoretically possible that the shortest path between two locations (PCs) could be computed (Muller et al. (1996)) if the recurrent PC connectivity represented pairwise distances in real space, but is not clear how such a mechanism could be implemented neurally. Notwithstanding these issues, PC remapping would mean that any learned vectors between two locations would need to be re-learned in each new environment (Bush et al. (2015)) such that this navigational scheme could only be useful in a local setting.

In contrast, GCs within a module are known to maintain their relative spatial offsets between environments and fire in a context independent manner. Bush et al. (Bush et al. (2015)) suggested how this feat could plausibly be performed both algorithmically and neurally (Marr and Poggio (1977)), but note that these solutions require the large scale regularity of all grid patterns in order to operate reliably. This is not obviously the case; GCs have been shown to stabilise slowly in open fields (Barry et al. (2012)) or environments with environmental boundaries (Carpenter et al. (2015)) or fail to form hexagonal patterns whatsoever (Derdikman et al. (2009); Fig. 1.1G). To date, no such study has categorically shown that spatial navigation is impaired during these periods where the GC representations are stabilizing.

Unsupervised learning and the successor representation

The observation of periodic but non-hexagonal GC firing patterns questions their applicability as ‘perfect’ path integrators, localizers or vector navigators although it is still possible that GCs may simply represent a useful but non-essential system for performing all or none of these functions. However, these peculiar deviations from the canonical grid pattern also re-open the question of how such representations might be initially formed.

One interesting possibility is that GCs may represent a low dimensional representation that might be relevant to some behavioural function. Dimensionality reduction techniques work on the principle of extracting the salient features of a data-set. By throwing away some of the less important features, the size of the representation can be compressed while still preserving most of the information in the data.

Perhaps the commonest of these techniques is PCA. PCA works by deducing the direction in a multi-dimensional data space along which there is most variability in the data. Given it’s simplicity and common usage, when Dordek et al. (Dordek et al. (2015a)) showed that performing PCA on a population of simulated PC rate-maps could produce striking periodic patterns, it was almost surprising that no one had thought to do so before. However, albeit reminiscent to the canonical grid pattern, vanilla PCA tends to produce square grid patterns. Moreover, the
authors also showed that thresholding the PC-GC weights to be positive transpired to be the key ingredient necessary to produce hexagonal patterns, a fascinating and unintuitive result (that was nonetheless also proven analytically) that the authors proposed might be related to the finding that GCs in mEC appear to be exclusively excitatory.

In parallel, Stachenfeld et al. \cite{Stachenfeld2014} had shown similar square-periodic grid patterns to emerge from work on the SR \cite{Dayan1993}. The SR was devised as a useful representation for supporting model-based RL. Without giving a full treatment of the field of RL (for a comprehensive introduction see \cite{Sutton1998}), the RL problem can be characterised as a set of states $s \in S$, a set of observations $o \in O$ associated with each state, a set of actions $a \in A$ which move the agent between states and a transition distribution $p(s'|s,a)$ which describes the probability of transitioning from state $s$ to state $s'$ given an action $a$. The goal of the agent is then to develop some state-dependent policy $\pi(a|s)$ which will allow it to move through space so as to maximize its cumulative future reward, which would be obtained by summing the rewards attached to each state at each timestep $R(s_t)$.

The essence of solving this problem is to learn the so-called ‘value function’, which assigns to each state a value equal to the cumulative future reward expected given that the animal is in the present state:

$$V_{\pi,\gamma}(s) = \mathbb{E}_\pi \left[ \sum_{t=0}^{\infty} \gamma^t R(s_t)|s_0 = s \right]$$

where $\gamma$ is a temporal discount factor that down-weighs the importance of rewards received in the future (when $\gamma = 1$, all rewards are treated equally; when $\gamma \in [0, 1]$, states occurring sooner in time are weighted higher). Importantly, the value of a state is inherently tied to the current policy. The transition matrix between all states in the environment is then defined as the product of the policy and the transition function $T_\pi(s,s') = \sum_a \pi(a|s)P(s'|s,a)$. The value function can be learned in a model-free fashion by following the current policy $\pi$ and incrementally updating the value of each state according to the difference between the expected reward and the reward actually received when transitioning from the current state. This describes the temporal difference (TD) algorithm \cite{Sutton1988} and is referred to as a ‘model-free’ strategy, since no information about the environment is explicitly learned (the transition function, which defines how the world will change in response to an action is not stored). These methods are typically fast and cheap to compute but are inflexible to changes in the environment or its reward structure. If the location of a reward is changed, revising a (deterministic) policy must necessarily involve several erroneous journeys to the now rewardless previous location of the goal. If a barrier is introduced, the animal must learn a new value function through
trial and error in order to then navigate around it.

In contrast, model-based methods learn an internal model of the environment (i.e. the transition structure). In doing so, an agent can perform 'planning', a process of offline inference which involves simulating trajectories through the environment in order to determine apriori which is the most likely to result in a reward, without wasting effort in actually experiencing these trajectories. If a goal location or environmental feature is changed, the agent can still plan the optimal trajectory. However, this flexibility comes at the cost of expensive searches through the space of possible trajectories.

However, the value function can be decomposed into a product of the reward function $R(s)$ (the expected reward in state $s$) and the SR matrix $M(s|s')$, where $M$ encodes the expected discounted future occupancy of state $s'$ given an initial state $s_0$:

$$M(s|s') = \mathbb{E}[\sum_{t=0}^{\infty} \gamma^t I(s_t = s')|s_0 = s]$$ (1.2)

where $I$ is an indicator function which return 1 if its argument is true and 0 otherwise.

Thus, the RL problem is decomposed into learning separated representations of reward and environment such that the resulting strategy possesses some desirable qualities of both model-free and model-based approaches. Firstly, policy evaluation is efficient, since the agent can choose an action by simply combining the pre-cached reward function and SR. However, if the reward structure is changed independently of the state dynamics, the value function can be rapidly re-computed. Moreover, the SR can be learned in absence of rewards whatsoever, such that if a goal is then introduced, a suitable behavioural trajectory can be rapidly deployed.

The SR is therefore a representation that supports efficient behavioural control through the RL framework, but how is it related to the hippocampus? The key insight that links this approach to that of Dordek et al. (Dordek et al. 2015a) is that both are effectively encoding a form of the transition structure of the environment. As discussed, PCA operates by inferring the most significant directions of variation in the $N$-dimensional dataset upon which it is operating. This is achieved by finding the eigenvectors (and corresponding eigenvalues) of the covariance matrix of the data. In the context of an agent navigating an environment where PCs fire with Gaussian tuning curves, the correlation between two neighbouring PCs can be interpreted as representing their transition probability. If two cells are nearby, the probability of transitioning to those cells is higher than if they were further apart.

Thus, the SR interprets PCs as not representing spatial location, but as the discounted expected number of times the location encoded by that PC will be visited given the current state. This leads to some interesting predictions, namely that
PC fields should be skewed in the direction of previous behavioural trajectories or be discontinuous across environmental despite the availability of sensory cues that might allow the animal to infer its current location. However, under a uniform trajectory in an open field, PC fields would be symmetric with a tuning function that decayed with distance from the encoded location. Stachenfeld et al. (Stachenfeld et al. (2014); Stachenfeld et al. (2017)) simulated an agent navigating in different environments and found the eigendecomposition of the SR produced GC-like representations. Moreover, the dominant eigenvectors of the SR are shown to vary with the discount factor $\gamma$, suggesting that larger grid scales could be used for planning over longer time-scales.

**GCs as representations for relational knowledge**

Although this discussion has focussed on the role of GCs in spatial computation, physical space is of course only one type of abstract space, albeit one that appears to be represented strongly in the hippocampal formation. Considering this, it is unlikely to be a coincidence that GCs and PCs were first discovered in the context of spatial mapping; the striking forms of their receptive fields can only be realized by correlating their firing with location in task space, which must be known to the experimenter. The suggestion that GCs and PCs may be involved in the encoding of non-physical space has only been recently investigated, but has resulted the discovery of similar signals in the visual cortex of both nonhuman primates (Killian and Buffalo (2018)) and humans (Nau et al. (2018); Julian et al. (2018)).

In one experiment, subjects were required to ‘navigate’ within a conceptual task space on a computer screen while being monitored in functional magnetic resonance imaging (fMRI). The task space was defined by a cartoon bird whose neck and leg length could be varied, defining a 2D ‘bird space’ (Constantinescu et al. (2016)). Navigation in this context was the action of changing these lengths and amazingly was shown to produce grid-like representations in the BOLD response using an analysis technique developed earlier to show grid-like activity in a virtual reality (VR) navigation task (Doeller et al. (2010)). A second study trained rodents to press a lever at a precise point in an ascending frequency (Aronov et al. (2017)). The experiments showed periodic 1D grid-like responses in the mEC when their firing was correlated with frequency.

Several studies have attempted to uncover the neural bases of PI, whether in the HPC (McNaughton et al. (1983)), mEC (Kropff et al. (2015b)) or upstream sensory regions. However, these recent findings pose the interesting question of what constitutes PI in non-physical space. To perform PI in abstract spaces, GCs would need to have some notion of velocity in these spaces, posing several important questions for the GC field. Firstly, are GCs flexible in their ability to encode different task dimensions? Secondly, do GCs discover these manifolds according to principles that
are task-dependent (reward based) or by some other principle (e.g. PCA). Lastly, is there a bias towards spatial over abstract representations in GCs and if so, does this bias give clues as to the evolution of these cells or does it simply reflect that physical space is disproportionately salient or useful?

The possibility that GCs may encode arbitrary abstract task spaces has prompted suggestions that the GC system may be optimised to store and perform relational computations on abstract concepts (Garvert et al. (2017); Behrens et al. (2018)). These arguments are similar in spirit to those made in the context of hierarchical location decoding and vector navigation; representing knowledge in hierarchical contextual space may be beneficial for performing efficient distance computations between concepts; that is to say, inference based on structure.

1.3 Summary and overview of investigation

1.3.1 An integrated view of GC function

Whether GCs represent an encoding of the environment’s transition matrix does not necessarily imply a role in RL; rather, this interpretation could in fact be considered as complementary to the traditional view of GCs as performing PI and the associated experimental evidence. In the SR / PCA view, GCs are generated entirely by input from PCs. However, as discussed there is significant evidence to suggest a bidirectional interaction (Evans et al. (2016)). In this light, rather than passively encoding a representation of the transition structure of the environment, it is suggested that GCs actively use this representation to PI and influence the firing of PCs.

Thus, I suggest that the most plausible theoretical and experimental hypothesis is that GCs should be driven both by PI and PCs, and that PCs should be driven by sensory inputs (possibly driven by BVCs) but also influenced by GCs. This framework would mean that GCs and PCs would react differently to environmental distortions, as was argued earlier in this section. Recent results from our own (Chen et al. 2018, under review) and other labs (Krupic et al. (2018); Campbell, Mallory and Giocomo, 2016, SfN) suggest that GCs and PCs may be more reliant on PI and sensory information, respectively.

1.3.2 Distortions to the canonical grid pattern

The perspective of this thesis is that this integrated view is important. A crucial limitation of all current models of GC firing and the first principal topic of this investigation is that no current model of GC firing can satisfactorily account for the distortion of GC firing patterns near to environmental boundaries (Stensola

\[ \text{Not necessarily in a Euclidean sense} \]
et al. (2015); Hardcastle et al. (2015)) or in non rectangular-environments (Krupic et al. (2015); Fig. 1.1H)). Models that focus on the role of GCs in performing pure PI ignore the fact that they, like PCs, are stable between repeated visits to an environment and are necessarily anchored to the environment. Models that focus on GCs as being formed exclusively by PCs do not consider that GCs appear to be performing some form of PI.

Specifically among these observed distortions, the shearing effect shown to be more prominent in larger environments and the possibly associated phenomenon of orientation offset to environmental features (Stensola et al. (2015); Krupic et al. (2015)) has not as of yet been accounted for. Whereas a low-dimensional encoding perspective can be shown to produce non-hexagonal firing in non-square environments or when poorly converged (Stachenfeld et al. (2017)) they predict that grids should be regular in a featureless square environment with no consistent orientation offset to environmental boundaries (Dordek et al. (2015a)).

Moreover, it is as of yet unclear whether these distortions play a functional role, or are simply the result of the imperfect operation of a complex interconnected system. The aim of the investigation is therefore to investigate how these distortions might arise through the interaction of GCs, PCs and BVCs.

The principal aim of this thesis is therefore to attempt to offer some possible explanations for these observations. In all our modelling, the origins of the grid pattern is not considered, focussing instead on how the canonical grid pattern might be distorted through the animal’s interactions with its environment.

1.3.3 Overview

Chapter 2 begins by asking whether the orientation offset and shearing distortions may serve a functional role. The interactions of GCs with environmental boundaries, mediated by PCs and BVCs, are considered. Specifically, I ask whether these distortions may arise firstly from a simple optimization of Hebbian learning to sensory inputs and secondly whether the resulting patterns might be useful from the perspective of location decoding. Importantly, these principles are agnostic of the underlying GC machinery and are instead based purely on the geometrical form of the GC firing pattern.

Chapter 3 attempts to extend the arguments made in chapter 2 within the context of a CAN model. Firstly, it is demonstrated that the the firing pattern of a population of GCs maintained by a static CAN model can produce characteristic shearing effects accompanied by orientations offsets, when driven b strong sensory inputs from PCs and subject to experience dependent rescaling (Barry et al. (2007)). However, these results are demonstrated to be difficult to translate to a full model of GCs performing PI. This result reveals an important limitation of current GC models, which consider
the influence of sensory inputs in a simplistic fashion. Moreover, it is concluded that the ‘hard-resetting’ model of GCs by sensory inputs is unlikely to produce the observed grid pattern distortions, nor is it an optimal scheme for learning in novel environments.

Chapter 4 details the development of a novel model of GC firing in which GCs maintain an estimate of location by optimally integrating information from PI and sensory cues from PCs. I show that this simple model of integration can account for several as of yet unaccounted for observed phenomena, including experience dependent distortions and global integration of local maps. Moreover, the model is able to learn sensory associations while navigating within a novel environment.

Chapter 5 builds upon an important limitation of the model from the previous chapter. Although capable of simultaneously learning and navigating in a novel environment, the conditions of convergence are relatively brittle and rely on relatively low PI noise. Firstly, the features of an ideal navigation and mapping system are explored, taking inspiration from engineering principles. Secondly, the previously described system is augmented, allowing it to perform offline inference in a neurally plausible manner. This process of offline inference is demonstrated to bear a resemblance to the phenomenon of hippocampal replay, suggesting a novel functional role and mechanistic explanation. This inference amounts to imbuing the system with the ability to reorganise observations in space given new information.

Chapter 6 discusses efforts to investigate the predictions made by the model in existing experimental data and presents a novel analytical technique for analyzing local distortions. Our analysis suggests that distortions to the grid pattern are highly non-local and may corroborate the mechanism proposed in chapter 4.
Uniform grid cell firing patterns have three principal axes of symmetry, each separated by 60° (2.1): In an environment with straight walls such as a square or rectangle, an angular offset relative to each of these walls can be defined for each of the three axes.

In the case of a square or rectangular environment, if one of the axes is aligned parallel to one of the walls, the remaining two will be offset by $90° - 60° = 30°$ (Fig. 2.1A). The minimum of these three relative offsets is defined as $A_{\text{min}} = \min([A_1, A_2, A_3])$ (since the six peaks in the sAC (see Appendix A.1) are 180° symmetrical) which for a uniform hexagonal GC firing pattern has a minimum and maximum of $0°$ and $15°$ respectively. It has been demonstrated (Stensola et al. (2015); Krupic et al. (2015)) that $A_{\text{min}}$ consistently clusters around $7.5°$ in square environments.

This specific angular offset suggests that GCs must align themselves according to the geometric properties of their environment and it is thought that this information may be mediated through BVCs, or indirectly through PCs. Moreover, this angular offset is preserved across all GCs with similar scale (i.e. each grid module), though the spatial phases of these GCs have been found to be uniformly distributed such that they provide an even coverage of the environment.

If GCs adopt a specific firing pattern in each environment, it’s possible that they could do so by forming direct associations with the cells providing sensory inputs. In Hebbian learning (Hebb (1949)), changes in synaptic connectivity between pairs of cells is assumed to be dependent on the correlation of their firing such that cells that fire together form excitatory connections and cells that fire distinctly form inhibitory connections, often stated in its most simple form as:

$$\tau_w \frac{dw}{dt} = vu$$  \hspace{1cm} (2.1)

where $w$ is a vector of weights between the pre-synaptic neurons whose activities are represented in the vector $u$ and the post-synaptic neuron $v$. $\tau_w$ is a constant
which can be interpreted as the learning rate or membrane constant of the neurons. However, the basic Hebbian rule is inherently unstable and numerous extensions have been devised such as covariance based rules, the BCM rule (Bienenstock et al. (1982)) and mechanisms involving both subtractive and multiplicative synaptic normalisation (Miller and MacKay (1994); Dayan and Abbott (2001)).

BVCs are known to fire at specific allocentric distances and directions to environmental boundaries, thought to represent the downstream processing of a number of higher sensory modalities. The investigation begins therefore by asking simply whether specific configurations (orientation, scale, spatial offset) of the GC firing patterns may be preferential for forming associations with BVCs. Importantly, the following chapter remains agnostic to the mechanistic generation of the grid pattern, rather the geometrical relationship between the GC and BVC firing patterns and their environment is used as a possible proxy for investigating more biologically plausible mechanisms of GC firing in Chapter 3.

### 2.1 Modelling GC and BVC firing patterns

The idealised firing patterns of GCs are well characterised by three parameters. The grid scale ($\lambda$) is defined as the distance between successive grid fields. The orientation ($\phi$) is defined as a rotation of the nearest grid axis counter-clockwise from the x-axis. The spatial offsets ($c$) are defined as a shifting along two of the grid axes, relative to a grid field in the bottom-left corner of the environment and have units of angular phase ($c=[c_1, c_2]$). The GC firing pattern is periodic along the directions of its principal axes with period $2\pi$, such that a spatial offset of $2\pi$ along any axis will produce the same pattern.

The latter definition becomes clearer when considering how the GC firing patterns are generated. This is most easily achieved by taking the product of three plane

![Fig. 2.1: $A_{\text{min}}$ (Stensola et al. (2015)) is taken as the smallest angular difference between any of the three grid axes and either the vertical or horizontal boundary. A $A_{\text{min}} = 0^\circ$. B $A_{\text{min}} = 15^\circ$. C $A_{\text{min}} = 10^\circ$. $A_3$ not shown, but would be $30^\circ$ anticlockwise of the left wall in A.](image-url)
waves separated by 120° (Fig. 2.2). Each plane wave is a cosine wave with wave vector $\mathbf{k}$ defined according to the desired orientation $\phi$:

$$k(\phi, \theta, \lambda) = \left( \frac{4\pi}{\sqrt{3} \lambda} \cos(\phi + \theta), \frac{4\pi}{\sqrt{3} \lambda} \sin(\phi + \theta) \right)$$  \hfill (2.2)

where a factor of $\sqrt{3}/2$ has been used to normalise $\lambda$ to the environment. Thus, setting $\lambda = 0.25$ and $\phi = 0$ will produce a GC firing pattern with 5 fields along the x-axis (Fig. 2.2). $\theta$ represents the angular offset. A single planewave is defined as:

$$b(\phi, \lambda, c, \theta) = 1 + \cos (k(\phi, \theta, \lambda) \cdot x + c)$$  \hfill (2.3)

The +1 ensures that the planewaves ensures that the resulting GC firing is positive. The desired GC firing pattern is then given by:

$$g(\phi, \lambda, c) = \prod_{i=1}^{i=3} b(\phi, \lambda, c_i, 120(i - 1))$$  \hfill (2.4)

In this analysis, BVCs are modelled simply as a decaying exponential, $b(x) = \exp(-\alpha |X - x|)$ with decay constant $\alpha$. For the purpose of simplicity, only four BVCs are considered, each with a preferred firing direction corresponding to one of the four environmental boundaries. Their maximum firing rates all occur at $x = 0, x = X, y = 0$ and $y = Y$, where $X$ and $Y$ are the box dimensions, as illustrated in Fig. 2.3.

2.2 Optimizing overlap between GC and BVC firing

Previous analyses investigating the orientation offset phenomenon have focused on elucidating relationships between $A_{\text{min}}^2$ and the intrinsic scale independently of the environment in which the GC firing patterns were observed (Stensola et al. (2015); Krupic et al. (2015)). However, given the evidence discussed previously, which

\footnote{A similar approach forms the basis of oscillatory interference models of GC firing (Burgess et al. (2007)).}
Fig. 2.3: BVCs are modelled as cells whose firing rates decay exponentially with perpendicular distance from walls at a preferred angle, with decay constant $\alpha$. Here, the firing rates of four BVCs are shown superimposed, with preferred angles of firing $\theta = 0 : 90 : 270^\circ$.

suggests that GCs are heavily influenced by the geometry of their environments in a manner that is possibly mediated by BVC interactions, it is possible that the relative scales of the environment and grid firing patterns might interact. Thus, in this chapter results are presented in terms of a dimensionless box-grid scale ratio $X/\lambda$, where $X$ is the length of the wall of the environment in equivalent units to that used to measure the grid scale.

In order to investigate whether a particular orientation might be the optimal solution to some Hebbian type learning objective, one would normally need to construct and simulate a full working model with GC-BVC connections. However, an approximate form of the problem is initially considered. Since Hebbian-based rules are inherently correlation based, it is asked simply whether a particular grid orientation might maximize some function of the total overlap (correlation) with a set of four BVC firing fields, defined as the integral of the two firing patterns across the environment:

$$\text{Overlap} = \sum_{b=1}^{N_B} \int_0^X G(x) \cdot B_b(x)$$

where $G(x)$ and $B_b(x)$ are the spatial firing rates of a given GC and BVC, respectively. GCs within a module are known to share the same scale and orientation but maintain their spatial offsets. Thus, it would seem unlikely that each GC in a module would adopt the same orientation and spatial offset by optimization on a single cell level. Rather, it seems more plausible that the GCs are optimizing their firing patterns on a population level. Thus, analysis begins by optimizing the Hebbian criteria across a population of spatially offset GCs, assuming each shares the same properties.

Orientations of the grid were only considered from 0:15°, since the amount of BVC-GC overlap is symmetric about each 15° interval and periodic about any 30° interval for a uniform hexagonal grid, an assumption that was verified in low resolution simulations. Later in this chapter this assumption is relaxed, allowing the grid to deform via a linear shearing process.
Fig. 2.4: Optimizing total grid cell - boundary vector cell correlations, defined as the sum of the product of their firing rates across space. A $A_{\text{min}}$ producing minimum overlap over offsets with four BVCs B $A_{\text{min}}$ producing maximum overlap over offsets with four BVCs. Both figures suggest that no optimal angle exists.

For all simulations in this section, the overlap in firing between each GC firing configuration and the BVC population was computed for all values of orientation and phase offset. For each of the simulations, spatial offsets were considered from $c_1 = c_2 = 0 : \frac{\pi}{16} : 2\pi$ rads (a total of $32^2 = 2014$ unique offsets) uniformly covering the environment. The box-grid scale ratio was considered from $X : \lambda = 1 : 0.2 : 10$ and orientation as $\theta = 0 : 0.25 : 15^\circ$.

2.2.1 Optimizing the total overlap

Firstly, the sum of the GC-BVC firing pattern overlaps across the environment are optimized. Fig. 2.4 shows the orientation that minimises (A) and maximises (B) the sum of the overlaps over all spatial offsets for a given GC with scale $\lambda$ and four BVCs with decay constants $\alpha$. Both plots show an approximately uniform distribution of $A_{\text{min}}$ values with no significant clustering about any particular orientation regardless of the scale.

This result might be expected, given that the equivalent operation being performed in the model is the spatial convolution of the GC firing pattern with the BVC firing. Given all possible spatial offsets, the GC module will provide uniform spatial coverage, which would be by definition invariant to linear transformations such as rotation or translation.

2.2.2 Optimizing the variance in GC-BVC firing overlap

Next, the analysis considers the variance in overlap over all spatial offsets. From a Hebbian learning perspective, this scenario considers the difference in the strengths of associations between each spatially offset GC and the BVC population, where zero variance in overlap would suggest the total synaptic strength from each GC to the BVC population would be equal, as might be expected if the total synaptic weight
from each GC were normalized by some homeostatic plasticity process (Turrigiano and Nelson (2004)). A large variance in the overlap might allow BVCs to maximally differentiate between their inputs at each spatial location. Such a configuration could plausibly arise from competitive learning between the GCs such that the strongest connections were accentuated and the weakest connections pruned.

**Simulation results**

Whereas the variance maximizing $A_{\min}$ values in Fig. 2.5B cluster about $0^\circ$, the variance minimizing values in 2.5A vary roughly inversely proportionally to the box-grid scale ratio, tending to a minimum at approximately $A_{\min} = 7.5^\circ$.

As was the case when considering the total sum of GC-BVC overlaps, the value of $\alpha$ has no significant effect on $A_{\alpha \min}$. Interestingly, the same qualitative behaviour applies for the case where $\alpha = 0$. When $\alpha = 0$, the BVC receptive fields do not decay from the boundary such that they are in fact uniform across space. The result then reduces to an optimization of the variance of the coverage of the GCs within a single module across the environment, independent of boundary inputs.

Examining the model more closely, Fig. 2.6B shows $A_{\min}$ to be approximately normally distributed about a mean of $7.5^\circ$, as reported experimentally (Krupic et al. (2015); Stensola et al. (2015)), although a second prominent peak is exhibited at $A_{\alpha \min} = 0^\circ$.

The decreasing trend begins at scale ratios greater than $X/\lambda = 4$. Below this value, the minima occur intermittently between $0^\circ$ and $15^\circ$, with the minima becoming less stable as the ratio increases. This finding suggests that the variance-minimizing orientation might not be stable enough to robustly attract the grid pattern in the presence of noise, leading to a distribution of values with a mean centered on that orientation. This would also explain how at small scales, Figs. 2.5A and B both show peaks at $0^\circ$. Interestingly, the minima are most stable at integer values of the scale ratio, whereas between integer values there appears to be almost no difference across $A_{\alpha \min}$ (Fig. 2.6C).

**Comparison to experimental observations**

To explore whether similar behaviour to that shown in Fig. 2.5A could be observed in existing data, analysis was performed on 343 GCs taken from two sources (Stensola et al. (2015); Krupic et al. (2015)), recorded in rat mEC in 0.9x0.9, 1x1, 1.3x1.3, 1.6x1.6 and 1.9x1.9 square environments. Each cell included in the analysis was classified as a GC according to author specific criteria.

When all cells from the combined dataset were considered in the analysis, there was no distinct decrease in $A_{\alpha \min}$ with increase in $X/\lambda$. However, a negative correlation begins to emerge as the sub-population of cells with a lower gridness score are
Fig. 2.5: Optimizing the variance in grid cell - boundary vector cell correlations, defined as the variance in the overlap of a given grid cell and four boundary vector cells, taken across the total population of all grid cells. A \( \alpha \) producing minimum variance in overlap over offsets with four BVCs B \( \alpha \) producing maximum variance in overlap over offsets with four BVCs. The scale ratio \( X/\lambda \) is used to denote the ratio between the box dimension and the grid scale. A predicts that as this ratio increases (grid scale becomes proportionally smaller), the optimal \( \alpha \) should tend towards \( 7.5^\circ \).

omitted from the analysis. Fig. 2.6 illustrates a trend similar to that observed in Fig. 2.5A. Notably, at lower scale ratios the \( \alpha \) values are approximately uniformly distributed, but become more clustered at \( X/\lambda > 4 \).

2.3 Distortions to the canonical GC firing pattern

Next, it was investigated whether GC firing pattern alignment was affected by deviations away from uniform hexagonality. Along with GCs, numerous other putative cell types have been reported which exhibit spatially periodic non-grid firing patterns (nonSPC) and spatially periodic non-hexagonal grid firing patterns (nonGC) (Krupic et al. (2012)). These include band cells (Krupic et al. (2012)) and ‘1D GCs’ observed on a linear track (Derdikman et al. (2009)).

In open environments (Stensola et al. (2015)), GCs have been observed to undergo a shearing-like transformation (Fig. 2.9A), which is defined as the local translation of an image by a distance and direction that is proportional to the perpendicular distance from a shear locus (centre). Moreover, this transformation was found to be absent upon first exposure to a novel environment but develop with progressive experience and was more pronounced in larger environments (Stensola et al. (2015)).

By performing either a uniaxial or biaxial shearing operation (Fig. 2.9A), the authors showed that the majority of non-uniform grid firing patterns could be returned to uniformity, eliminating the distortions. Moreover, previously offset GC patterns tended to re-align to one wall of the environment following the same correction, suggesting that the shearing and orientation offsets might be causally linked.
Fig. 2.6: A Data from [Krupic et al. (2015)] and [Stensola et al. (2015)] showing $A_{\min}$ against scale as a proportion of length of one of the sides of a square environment. Left: Error bars calculated by binning data into $\Delta X = 0.5$ intervals. Regression line calculated on unbinned data. Minimum gridness score $G_{60,\min} = 1.0$, bin-width $= 0.5^\circ$. Right: Histogram of $A_{\min}$ values across all scales shows mean value close to $7.5^\circ$. $A_{\min}$ producing minimum variance in overlap over offsets with four BVCs. B Histogram of $A_{\min}$ values minimising variance over offsets across all scales $X/\lambda \in [0.1, 12]$, $\alpha = 3$. Red dashed line shows position of circular mean. D $A_{\min}$ producing maximum variance in overlap over offsets. Change in variance vs. orientation is much larger when the grid is of an integer scale.
2.3.1 Orientation offset and shearing as a local maximum in GC-BVC association

To test this hypothesis, the analysis next considered whether similar Hebbian optimality analyses could be used to produce shearing distortions to the GC pattern. However, adding the possibility of a 2D shearing transformation adds four additional parameters (the 2D shear centre and magnitude), making brute force optimization over a total of six parameters (including scale and orientation as before) infeasible for a reasonable range of parameters.

Of course, any computational difficulty would likely translate to the neural case; finding the global optimum of some cost function would also be a difficult task for a population of GCs. This task becomes even more difficult when considering the relative shallowness of the optimum observed in Fig. 2.6D. Instead, it might be more plausibly expected that GCs settle in some local minimum, which would necessarily be sensitive to the initial configuration.

Novelty dependence and anchoring

The density of PC coverage is thought to be related (O’Keefe and Conway (1978)) to the saliency of their preferred firing locations, clustering more densely near boundaries, entry ways (Muller and Kubie (1987a); Spiers et al. (2013)) and goal locations (Hollup et al. (2001)) than other points in a given environment. Moreover, when Stensola et al. (Stensola et al. (2015)) applied the corrective shearing operations to the distorted grid patterns, the most effective transformations were consistently found to be centered about one or two points (depending on whether they were uni-/bi-axial transformations), most often located in the corners of the environment.

Interestingly, the authors note that each animal was always introduced to the environment in the same corner, raising the possibility that PCs in these locations contribute strongly to the formation of the grid pattern. It is possible that upon initial exposure to the environment, the rapidly formed GC firing patterns form a strong connection with a small number of place fields located in the corners of the environment. Given the adopted configuration on first exposure to the environment, experience dependent optimization might be anchored by these strong initial associations.

Grid distortions as local optima

Given these observations, it was hypothesized that distortions to the GC pattern might represent local minima in an experience-dependent process of Hebbian optimization, given an initial starting configuration. This process was simulated by allowing the GCs to iteratively optimize their properties, assuming the grid pattern to be initially aligned to one wall of the environment.
In all simulations, GCs were initially aligned to one of the walls, reflecting experimental observations in novel environments. The initial shear centre was set to the corner of the environment, but was optimized along with the other parameters during the simulation.

### 2.3.2 Maximizing overlap with a single GC

Firstly, an analysis was conducted on a single GC, optimizing the properties so as to maximize overlap with a set of four BVCs. Unlike in the previous analysis, the grid scale was also optimized in addition to the orientation, spatial offset, shear centre and magnitude. Interestingly (Fig. 2.7A), the single GC adopted a discrete set of spatial scales into which it ‘snapped’ from its initial starting scale, which was varied over a continuous range. A small amount of shearing was present, although the shear centre did not change from its initial position in the bottom-left corner. Changes in spatial offset and orientation were negligible, which might be expected given that the BVC fields fire at a maximum at the walls.

$A_{\text{min}}$ was extracted from simulated ratemaps generated from the optimized properties (see Appendix). As hypothesized, the shearing transformation was sufficient to generate the appearance of orientation offset in absence of an intrinsic rotation. The effect on $A_{\text{min}}$ was even more pronounced when fixing the initial scale (2.7B). In this case there was much more variability in the shearing magnitude, although changes in spatial offset, orientation and shear centre were again negligible. Although $A_{\text{min}}$ oscillated dramatically with the scale ratio, the resulting offset was limited to approximately $6^\circ$ resulting in a qualitatively similar but shifted histogram to that observed experimentally (Stensola et al. (2015); Krupic et al. (2015); see inset histogram in Fig. 1.1C, right).

### 2.3.3 Minimizing variance over a population of GCs

Next, the previous minimization of variance in overlap was re-analyzed in the context of the dynamic optimization process, considering a population of 100 GCs with uniformly distributed spatial offsets. Again, the scale was initially allowed to vary, again resulting in a set of different but discrete values (Fig. 2.8). In contrast to Fig. 2.7A, varying the scale was completely sufficient to minimizing the variance in overlap across the population such that the grid pattern remained undistorted (Fig. 2.8A).

However, when the grid scale was fixed (Fig. 2.8B), the population of GCs underwent considerable shearing, this time resulting in $A_{\text{min}}$ values which oscillated with scale ratio, tending to $7.5^\circ$ as the scale ratio increased (grid scale decreases). The distribution across all scale ratios showed a peak in the histogram centered on $7.5^\circ$ (Fig. 2.6), qualitatively matching the experimentally observed distribution.
Fig. 2.7: Experience-dependent maximization of Hebbian overlap with a set of four BVCs with decay constant $\alpha = 5$ for a single GC. Beginning with a grid field in one of the corners of the environment, the grid properties are optimized via gradient descent until a local minimum is reached. A When the grid scale is optimizable, discrete grid scales become preferable with some shearing. B When scale is fixed, shearing is more pronounced. In both cases, changes in orientation and offset were negligible. Note that $X/\lambda_\infty$ and $X/\lambda_0$ are the steady state observed and intrinsic scale ratios, respectively.

Fig. 2.8: Experience-dependent minimization of variance in Hebbian overlap with a set of four BVCs with decay constant $\alpha = 5$ for a population of GCs. The grid properties are optimized via gradient descent until a local minimum is reached. A When the grid scale is optimizable, discrete grid scales become preferable with no accompanying shearing. B When scale is fixed, shearing is more pronounced. In both cases, changes in orientation and offset were negligible. Amplitude of $A_{\text{min}}$ oscillations tend to $7.5^\circ$ as $X/\lambda$ increases (smaller grid scale). Note that $X/\lambda_\infty$ and $X/\lambda_0$ are the steady state observed and intrinsic scale ratios, respectively.
2.3.4 Analysis of optimized scale changes

Next, the same scale changes that arose from the two optimization processes in Figs. 2.7A and 2.8A were examined in more detail. Visually, both simulations appeared to show discrete sets of scales which increased in an approximately geometrical fashion (i.e. with a fixed scale ratio). To test the hypothesis, the optimized scales were first clustered into \( k \) groups (number of clusters chosen visually, indicated on figures). The ratio between cells in successive clusters were then computed and visualized in Fig. 2.10 (middle column).

Both distributions showed multiple peaks, although ratios between smaller scales tended to share a similar scale ratio as shown by the ratio between the means of successive columns (red lines in 2.10 middle column red dashed lines).

The scale ratio was larger in the minimization of variance than in the maximization of overlap, but both simulations showed scale ratios in the range \( X/\lambda \in [1.3, 2] \). Moreover, the similarity of the ratio between the means of successive clusters suggested an approximately geometric progression of scales. Interestingly, the range of scaling ratios and apparent geometric progression approximately match the scale of experimentally observed modules (Hafting et al. (2005)).

Finally, it was explored whether the observed experience-dependent optimization of scale could account for experimental observations that the scale of the grid pattern tends to temporarily increase upon exposure to a novel environment (Barry et al.)
Fig. 2.10: Analyses of scale changes when maximizing overlap (A) and minimizing variance in overlap (B). Both optimizations show a clear preference for a discrete set of scales. **Left** Discrete scale clusters. **Middle** Histogram of ratios between in scales in successive clusters. Red dashed lines show ratios between successive cluster means. **Right** Change in scale as a function of original scale.

However, the simulation results did not match exactly the experimentally defined phenomenon. Firstly, in the optimization process GCs tended to change their scale so as to match the nearest of a discrete set of grid scales, which meant that the scale could both decrease and increase following the optimization (Fig. 2.10, right column), whereas only temporary expansions have been observed experimentally. Secondly, novelty-induced expansions in scale tend to be followed by a re-contraction to the originally observed scale over subsequent experimental trials.

It is unclear how to interpret these details in the context of the optimization result. However, the results do predict that the grid scale should be modulated by the size of the environment, such that unilateral expansions should produce concomitant expansions in the grid scale.

### 2.4 Environmental effects on shearing in existing data

Given the results from the previous section, existing GC data was re-analyzed (Stensola et al. (2015); Krupic et al. (2015); Barry et al. (2007); Barry et al. (2012)) to examine further the relationship between the orientation offset and shearing. To measure the magnitude of shearing in experimentally observed ratemaps, the ellipticity metric (Stensola et al. (2015)) was computed for each grid pattern.
2.4.1 Ellipticity as a metric for shearing

In the sAC of a uniform hexagonal grid, a circle can be transcribed through the six nearest peaks surrounding the central peak (the autocorrelation at [0,0] offset). If a shearing transformation is applied along one or two perpendicular axes to the original rate map, the circle fitted to the peaks of the sAC will become skewed along one or both direction, producing an ellipse. Thus, the distortion can be characterized by the ‘ellipticity’ or ‘eccentricity’ of the resulting ellipse, both of which are functions of the ratio of the semi-major \( r_a \) and semi-minor \( r_b \) axes. These semi-major axis is defined as half the diameter of the ellipse at it’s widest point whereas the semi-minor axis is perpendicular to the semi-major axis and by virtue of the properties of the ellipse, measures half the narrowest width of the ellipse. The ellipticity is then simply defined as:

\[
\text{Ellipticity} = \frac{r_a}{r_b} \tag{2.6}
\]

where \( r_a \) and \( r_b \) are the semi-major and semi-minor axes of an ellipse (widest and narrowest dimension, which are necessarily at right angles). In a circle, the ratio of the two axes would be 1, however in an ellipse the ratio will always be \( \frac{r_a}{r_b} > 1 \).

Details of the ellipse fitting procedure can be found in the section appendix. Examples of fitted ellipses are shown in Fig. 2.11, along with error in the fitting process, defined as the total of the residual distances between the ellipse and the six inner peaks to take into the account the possibility that the GCs were deformed by a non-shearing transformation.

2.4.2 Correlations between grid distortions and Amin°

As might be expected, there was a clear negative trend between the gridness score and ellipticity measure (Fig. 2.12 top-left). However, this correlation was not as strong as might be expected, possibly reflecting the fact that GC firing patterns may have a low gridness score if the fields are less defined, incorporating background noise even when their fields are distributed in a non-elliptical hexagonal pattern. The ellipticity measure doesn’t consider the coherence of the firing ‘image’ (the shape of the fields), as it relies only on the coordinates of the centroids of the firing fields (checked by manual inspection).

Firstly, Fig. 2.12A shows figures reproduced from Stensola et al. (2015). The rightmost figure shows a clear trend between the optimal shear parameter for the corrective transformation and the original grid orientation. The authors note that following the shear transformation, the orientation offset was significantly reduced (peak for \( A_{\text{min}} \) at -0.9°, s.d.: 6.6°; \( A_{\text{min}} \) before versus after shearing: \( Z=10.7, P=7.4\text{e-27} \)).
There was a broad positive correlation between the ellipticity metric and $A_{\min}^\circ$ (Fig. 2.12, middle- and top-right). However, no such pattern was clear from the equivalent plot of gridness score against $A_{\min}^\circ$, although there appears to be greater clustering towards values of $0^\circ$, $5^\circ$ and $10^\circ$ values for gridness scores greater than 0.75. However, a histogram showing the population of cells split into two subpopulations (Fig. 2.12, Bottom-right) at the 85th percentile shows that this effect was not pronounced enough to be convincing, other than a distinct peak at $4^\circ$ – $6^\circ$. These findings may reflect limitations of the dataset; there were relatively few examples from large environments ($X_{\max} = 1.2$m).

2.5 Chapter summary

The analyses in this chapter explored whether GC firing patterns might consistently become misaligned to either boundary of a square environment through Hebbian-like interactions with BVCs and PCs.

Following a preliminary analysis of the experimental data, the analysis attempted to elucidate in further detail the specific conditions under which the offset might arise. Current work has focused on analysing the effect without taking into serious consideration the relationship between the geometry of the environment and the properties of the GCs. In contrast, it was hypothesized that if GC firing patterns were aligned through their interaction with environmental boundaries, these differences should be evident by studying the alignment with respect to the relative environment and grid properties.

Initially, the analysis considered a population of GCs forming a complete GC module. Simulations suggest that the $7.5^\circ$ offset could arise so as to minimize the variance across all GC-BVC associations within that module if the grid scale were within a
Fig. 2.12: Middle-left: GC firing patterns with a higher gridness score have lower ellipticity. Middle-middle: Gridness and ellipticity scores have little effect on $A_{\text{min}}$. Middle-right and bottom-right: Histogram of data split into two populations. Top and bottom show the same plot for different gridness thresholds. GCs with a higher gridness score appear to be slightly less uniformly distributed than GCs with lower scores. Bottom-left: In our analysis, gridness was not strongly correlated with $A_{\text{min}}$. 
specific range in proportion to its containing environment. However, this result was shown to be unrelated to the specific form of the BVC fields, instead being related to the ‘coverage’ of the grid fields within the environment. Analysing a collated dataset of GCs in square environments with a range of box sizes, there was some evidence that the data supports the theoretical prediction. At lower scale ratios, the distribution of $A_{\min}^0$ values was approximately uniform, whereas at higher scale ratios, $A_{\min}^0$ tended to cluster around a smaller number of discrete locations. Confirming this correspondence is made difficult by the relative absence of data from GCs with small scales in large environments, such that the scale ratios exceed $\frac{X}{X} 5$.

However, the simulation results showed this minimum to be relatively shallow such that optimization to this exact configuration would be difficult for a system with inherent noise, neural or otherwise. It was therefore attempted to constrain the investigations to investigate more biologically relevant and behaviourally specific scenarios under which the offset might arise.

Moreover, the investigations to this point had considered the case of uniform hexagonal GC firing patterns. However, inherent in the question of alignment is the finding that GC firing patterns undergo an experience-dependent distortion. Applying an inverse shearing transformation to reduce the ellipticity of the grid patterns was also found to remove the orientation offset (Stensola et al. (2015)), suggesting that the two processes were causally related. Lastly, the corrective transformations were centered about the corners of an environment. Other than being spatially salient locations in the environment (the intersection of two walls is presumably more distinguishable from an arbitrary point along a featureless wall), the authors note (Stensola et al. (2015)) that the animal was always introduced to the environment via the same corner. It was hypothesized that the corner of the environment might play a role in anchoring an experience-dependent shearing transformation that produced an orientation offset in the resulting grid pattern.

Testing this hypothesis, the local optimization of two criteria was simulated; a) the maximization of total overlap for a single GC and b) the minimization of total variance in overlap across a population of GCs. The optimization was allowed to proceed via gradient descent from a starting configuration where the GCs were aligned to the wall of the environment, with shear centre at the corner.

Firstly, when allowing the GCs to optimize their scales, the grid patterns either expanded or contracted to the nearest of a set of discrete scales. These scales increased in a geometric fashion with a multiplicative factor that was similar to that observed experimentally. In the case of maximizing the total overlap, significant shearing was observed, however the resulting degree of orientation did not approach the values observed experimentally. However, when minimizing the variance across
the population as in earlier simulations, when the scale was also fixed the orientation offset $A_{\text{min}}$ oscillated and tended towards 7.5 as the scale ratio increased (as grid scale decreased).

Together, the results suggest that a shearing transformation applied about the corner of an environment may be optimal for minimizing the variance between a population of GCs and a set of BVCs. Moreover, the results predict that a unilateral expansion in the environment should produce concomitant scaling in the grid pattern. Although this behaviour has been demonstrated [Barry et al. (2007); Stensola et al. (2012)], it is difficult to isolate this hypothesis from the possibility that grid patterns are simply driven by PCs or BVCs which might also scale with the environmental transformations. Later chapters will explain this possibility in more detail.

It was not clear whether the experience-dependent optimization could explain the observations that grid scales temporarily expand on first exposure to an environment [Barry et al. (2012)] both expansion and contraction to a fixed set of scales was observed. More generally, it raises the question as to whether the observed expansion is a driver of the shearing process or is itself driven by the shearing. Future simulations might frame the problem slightly differently; given a gradual contraction in scale (from an initial expansion), the GC module might dynamically realign so as to maximally preserve existing GC-BVC associations, formed on initial exposure to the environment.

Lastly, the simulations were chosen deliberately not to impose a penalty term on the shearing and rescaling of the grid pattern. This equates to making no assumptions about the 'preferred' form of the grid pattern; however, it might plausibly be argues that any shearing transformation or rescaling away from some 'intrinsic' grid scale might be energetically unfavourable. However, it is difficult to justify this constraint while remaining agnostic to the mechanistic underpinnings of the grid pattern and more difficult still to balance the effect of such a constraint against the optimization of the designed criteria.

**Final conclusions**

In summary, this chapter developed a number of approaches to asking whether the alignment offset phenomenon might arise through a Hebbian-like optimization of GC-BVC associations. However, when only considering uniform GC firing patterns, it is difficult to assess whether any results is noteworthy, or whether it is simply the case that the phenomenon will inevitably arise out of some models given the narrow range of values that $A_{\text{min}}^o$ is constrained to take.

Moreover, the relatively simplistic treatment of the distortion processes as shearing transformation may well not be capturing the full nature of the distortive processes at play. Both the ellipticity and orientation measures are based around the central
peaks of the autocorrelogram. In larger environments, it was shown (Stensola et al. (2015)) by performing local analyses on quadrants of the grid pattern that these distortions are not local. The same may well be true of grid patterns in smaller environments. However, the analysis is justified on the basis that this simple transformation captures a large proportion of the observed distortion and accompanying orientation offset. A promising direction of further investigation would be to develop a more detailed method for analyzing local distortions.

It was not demonstrated conclusively whether different modules undergo shearing to a different degree. If alignment and distortion were different between modules, it would raise interesting questions over a number of GC decoding modules. Briefly, many models of location estimate rely on a top-down (largest grid scale) readout of position being successively refined as these 'larger-scale' readouts are combined with GC modules with smaller scales (Mathis et al. (2012); Towse et al. (2014); Mathis et al. (2015); Vago and Ujfalussy (2017)). This is due to the inherent periodicity of the GC system; it is only ever possible to estimate ones position up to the scale of the largest grid. In contrast, the accuracy of your position decoding is governed by the scale of the smallest grid. Thus, a number of theories have emerged to suggest that an optimal ratio of grid spacing might exit in order to optimally decode location, with regards to various 'accuracy' metrics. Notably, in the work of Mathis et al. (Mathis et al. (2015)), the decoding mechanism is able to compensate with independent distortions among GC modules, as long as the distortions are consistent across all GCs within a single module.

More generally, further experimental and theoretical work should focus on whether these departures from the canonical grid pattern are functional or a byproduct of an imperfect system. That is to say; if the GCs’ perception of space was distorted; the firing fields would be placed according to a 'perceived' hexagonal pattern, but due to errors in localisation within the environment, these firing fields would appear at different location to where they were intended in the real-world readout. Alternatively, if hexagonal firing patterns arise out of the need to encode information about the environment or the animal’s location within it (Dordek et al. (2015b); Stachenfeld et al. (2014)), it is possible that other representations, periodic or not, might be adopted to encode atypical information.

Lastly, this chapter was concluded by highlighting that these results are all agnostic to the underlying mechanism generating the grid pattern. The next chapter attempts to translate these results to a continuous attractor model of GC firing.
3. LOCAL ELLIPTICITY AND ALIGNMENT IN A CONTINUOUS ATTRACTOR MODEL OF GRID CELL FIRING

In Chapter 2, it was investigated whether specific, predefined linear transformations to the uniform hexagonal GC firing pattern might optimize a Hebbian-like process of BVC-GC association. Although the simulations considered both individual and modules of GCs, they were agnostic to the biological mechanism underlying the generation of the grid pattern, neither did they consider possible interdependence between GCs within a given module.

Moreover, the putative shearing process (Stensola et al. (2015)) was applied geometrically and did not consider possible underlying mechanisms that might produce such a transformation. In reality, the distortive effects observed in the grid patterns, which resemble a shearing process and whose effect can be described conveniently in terms of induced ‘ellipticity’, are likely to be the result of complex interactions between the pattern generating GC network and its sensory inputs (which seem to be most prominent near the boundaries or corners of an environment). This assumption is further evidenced by numerous other distortions to the idealised GC firing patterns, such as a reduced spatial coherence near to boundaries (Hardcastle et al. (2015)) and local scaling of the grid pattern in non-rectangular environments (Krupic et al. (2015)).

Of the existing mechanistic models of GCs, CAN models more than others provide a cohesive account of the ‘modular’ interactions between populations of GCs sharing the same scale and orientation. Thus, this chapter begins by attempting to develop some of the approaches from chapter 2 within the context of a CAN model, modelling the effect of sensory inputs as mediated by BVCs and PCs. The second part of the chapter outlines some limitations of existing GC models that were apparent by these analyses.

### 3.1 Methods

In contrast to OI and other models, which assume that a single GC is sufficient to produce the grid pattern, the central feature of CAN models is that this pattern arises solely as a result of the interactions of a population of recurrently connected GCs within the same module. CAN models rely on locally centered connectivity
schemes whereby spatially (in the sense of their firing fields in real-space) adjacent cells are mutually excitatory whereas cells separated in spatial phase are inhibited. Under certain conditions, this arrangement leads to the spontaneous establishment of a hexagonal pattern of activity on the ‘neural sheet’, which will henceforth refer to an abstract organisation of GCs in the brain, topographically mapped to their spatial proximity of their firing fields in physical space.

In a translation invariant network with spatially uniform and locally symmetric connectivity, the hexagonal pattern will remain stationary on the manifold in the absence of external inputs, moving only in response to noise. With the addition of direction sensitive asymmetry in the connection weights the same network becomes capable of performing path integration, translating the previously static pattern in proportion to the movement of the animal in space (Zhang (1996)). However, the same neuronal noise in addition to noise associated with the PI signal will cause the true location of the activity pattern to fall out of synchrony with the true animal location. This noise is the source of the aforementioned drift in CANs, meaning that they must receive a stabilizing external input in order to effectively maintain a position estimate.

### 3.1.1 Mapping

If the pattern remained static at all times, the readout (a particular cell’s activity plotted against the animal’s position in real-space) of a particular cell would be
uniform across all space. However, in CAN models the attractor pattern is ‘shifted’ across the manifold according to the movement of the animal. Thus, as the animal moves to a different location in real-space, a separate subpopulation of cells will become active while other subpopulations are silenced.

Thus, assuming that the pattern is translated in perfect correspondence to the animal’s movement, the pattern of firing on the neural sheet will be perfectly mirrored into spatial firing patterns in real-space, regardless of the form of the underlying pattern. The central assumption of the modelling in the first section of this chapter is that any distortions in the underlying pattern would also be mirrored in the real-space mapping, which might provide a model for the experimentally observed distortions in GC firing patterns.

However, the firing patterns in neural- and real-space are of course scaled versions of one another. This is achieved by a velocity gain factor which, treating the abstract neural space as having dimensions of $N_X \times N_Y$ cells, would have units of $v_m (\text{cells/m})$. It is an open question whether the grid scale in the biological case is indeed modified by a putative ‘gain factor’ (Giocomo et al. (2011)) or by structural properties of the GC module such as the number of cells.

3.1.2 Periodicity in the Neural Manifold

Multi-bump attractor pattern with tapering boundaries

In order for a grid module to perform PI, the neural manifold needs to be able to smoothly and continuously support the translation of the static attractor pattern across its surface. In multi-bump solutions, the hexagonal pattern is present in static form as the activity of GCs on a neural ‘sheet’ (Fig. 3.1B; Burak and Fiete (2009)). The hexagonal pattern is produced by virtue of the recurrent dynamics of the GC population. Each GC has a distance dependent outgoing connectivity profile such that GCs that are proximal on the sheet are excited whereas more distant GCs are inhibited. This connectivity results in distinct regions of activity and inactivity. Energetically, the optimal configuration for the organization of distinct activity regions is in a hexagonal lattice, a result closely related to the circle-packing problem. In this thesis, ‘periodic’ connectivity refers to a weight configuration in which the cells at one edge of the ‘neural sheet’ connect to the cells on the opposite edge. ‘Aperiodic’ connectivity does not have these connections, such that the sheet will have ‘edges’. Burak and Fiete (Burak and Fiete (2009)) showed that both periodic and aperiodic manifolds can support translation of these bumps.

Periodic manifolds have the disadvantage that they constrain the shape of the attractor pattern (Fig. 3.1E); since the pattern must be continuous across the edges, the pattern will be distorted unless its scale is an integer multiple of the size of the sheet, and the sheet itself has dimensions with a ratio of $[X, Y] = [1, \sqrt{3}/2]$. The
distortion could in principle also be corrected for by applying an appropriate gain transformation to the velocity input.

PI is achieved in aperiodic manifolds by tapering the net excitatory drive to the neural sheet smoothly to zero at its edges. This is achieved by imposing a smoothly fading circular weight profile (Fig. 3.1A). In this formulation, as fields move towards the edge, their firing fades out, while at the opposite edge fields spontaneously fade in by the same mechanisms that leads to establishing the grid in the centre of the sheet. These new fields are forced by the recurrent connectivity to appear in phase, allowing the pattern to be translated indefinitely. Burak and Fiete (2009) report than in the aperiodic case, attractor state (bump) movement is not completely translation invariant as edge effects to some extent continue to influence the activity in the centre of the sheet. The consequence for models of movement tracking via velocity and direction dependent input from head direction cells is that below a minimum animal velocity, pattern translation is ‘sticky’, although the effect can be minimised by increasing the size of the environment and providing a more gradual taper towards the edges.

3.1.3 Single bump attractor with twisted torus periodicity

Rather than assume a base static pattern in hexagonal form, a hexagonal readout (i.e. a firing pattern in physical space) can also be achieved by translating a single bump of activity across a manifold with specific connectivity. In a simple periodic manifold (with right-left and top-bottom edges connected), translating a single bump would produce a square lattice in the readout. Whereas the former connectivity scheme can be visualized as a torus, by first rotating the sheet by $180^\circ$ and connecting opposing edges one can construct a ‘twisted-torus’ (Fig. 3.1F; Guanella et al. (2007b)). Visualizing a square sheet, an activity packet translated off the left edge would re-appear on the right edge with the same vertical component. However, translating the packet off the top edge would cause it to re-appear on the bottom edge, but shifted by half the width in the horizontal direction (Fig. 3.1F). The result is a hexagonal pattern in the readout.

3.1.4 Temporal Dynamics

Simulations assumed a rate based network of neurons where the instantaneous firing rate of each cell is related to its membrane voltage by:
\[ \tau \frac{dV_i}{dt} = -V_i + \sum_{j \neq i} N \cdot N \sum_{j \neq i} W_{ij} F_j + P_i + B_i + \epsilon_i \]  
Multi-bump \hspace{1cm} (3.1)

\[ \tau \frac{dV_i}{dt} = -V_i + \left( \frac{1}{\sum_i V_i} \right) N \cdot N \sum_{j \neq i} W_{ij} V_j + P_i + B_i + \epsilon_i \]  
Single-bump \hspace{1cm} (3.2)

where \( \tau \) is the membrane time-constant, \( V_i \) and \( F_i \) the membrane voltage and firing rate of GC \( i \), \( W_{i,j} \) a weight matrix containing the recurrent connectivity strengths between each pair of GCs and \( \epsilon \sim N(\mu, \sigma^2) \) a Gaussian noise term. \( P_i \) and \( B_i \) represent input from either PC or BVCs. Normalization is achieved differently in both schemes, the multi-bump configuration relying on a sigmoidal activation function (Fig. 3.1C):

\[
F(V) = \begin{cases} 
0 & \text{if } V < 0 \\
F_0 \frac{1-e^{-V/2}}{1+e^{-V/2}} & \text{if } V \geq 0 
\end{cases} \hspace{1cm} (3.3)
\]

where \( F_0 \) is the maximum firing rate and the factor \( V/2 \) determines the gradient of the transition from 0 to 1. The firing rate for cells with a membrane voltage of less than 0 is set to 0. The single-bump solution relies on divisive normalization by the sum of the previous activity. The \( P \) and \( B \) terms represent external input to the manifold by PCs and BVCs respectively.

### 3.1.5 The Connectivity Profile

The stable attractor state reached by the network is related to the minimization of the potential energy (Hopfield [1982]) of the system. When the attractor state is reached, the rate of change of the dynamics of the system is zero (\( \frac{dV}{dt} = 0 \)). The spontaneous emergence of a static hexagonal pattern is predicated on the existence of a mexican-hat type connectivity scheme, whereby neighbouring cells in close proximity are mutually excitatory, whereas cells further away are inhibitory. As discussed in the introductory chapter, the exact mathematical shape is not particularly important and a number of schemes have been shown to support stable activity patterns. The only difference between the single- and multi-bump solutions is that in the latter, inhibition eventually decays to zero, at which distance another activity bump may form. In the former, inhibition does not decay such that only a single bump of activity can win out. For convenience, the exponentially decaying cosine model of Fuhs and Touretzky was adopted for the multi-bump solution (Fuhs and Touretzky [2006]), and a simple Gaussian function for the single bump solution (Guanella et al. [2007b]):
\[ W_{ij} = A \cdot \cos \left( \frac{2\pi \Delta_{ij}}{\lambda} \right) \cdot e^{-\frac{\alpha ||x_i - x_j||}{\lambda}} \] (3.4)

\[ W_{ij} = A \cdot e^{-\alpha ||x_i - x_j||_H^2} \] (3.5)

where \( A \) is the maximum strength of a synaptic connection, \( \alpha \) the decay constant and \( \lambda \) the grid scale. The effect of varying the decay constant \( \alpha \) is illustrated in Fig. 3.1D. \( || \cdot || \) is the Euclidean distance between cells \( i \) and \( j \) on the sheet. For the twisted-torus, the distance metric \( || \cdot ||_H \) is defined as:

\[ ||x - y||_H = \min_{i=0:6} ||x - y - \lambda \cdot \left[ \cos \left( \frac{i\pi}{3} \right), \sin \left( \frac{i\pi}{3} \right) \right] || \] (3.6)

Stated ore simply, eq. 3.6 states that the distance between two points on a sheet can be obtained by first tiling the second point to six adjacent ‘unit regions’ and calculating the Euclidean distance to each of these tiled points. The ‘twisted-torus’ distance is then the minimum of these six distances. To given an example, given two points on the left and right edge of Fig. 3.1F, the rightmost point would be tiled to the equivalent position on sheet immediately left of the original sheet, placing it near to the original leftmost point.

### 3.2 Dynamic contraction of the static pattern in a multi-bump scheme

There are two possible hypotheses that might explain the shearing of the grid pattern. The simplest is to assume that the static pattern is itself sheared and that this pattern is translated according to animal movement, as discussed. The second possibility is that the static pattern is unperturbed, but imperfect PI causes the readout pattern to distort. This chapter begins by assuming the former, asking whether the static grid pattern could be transformed in such a way as to produce a sheared readout under perfect PI.

As discussed, in CAN models, the uniform hexagonal firing arises from radially symmetric local connections between each cell and the others on the neural sheet. Clearly, to produce an equivalent sheared pattern as an attractor state would require this connectivity scheme to be modified such that the connectivity were elliptically rather than radially symmetric. If the weight profile were described by a bivariate Gaussian, this situation would equate to non-zero off-diagonal elements in the covariance matrix.

Maintaining the assumption that the GC system ‘prefers’ to adopt a uniformly hexagonal pattern, the connectivity scheme would then need to adapt to the the
context of each environment. Such a possibility seems unlikely given the precise nature of the connectivity and relatively short timescales across which this adaptation would need to occur.

However, applying stimulation will in general force a network away from its equilibrium state, which corresponds to the lowest energy configuration given the static connectivity (Hopfield (1982); Amit (1992)). If the stimulation is transient and not too disruptive, the network may return to its previous preferred state when it is removed. If it is persistent however, as might be the case if the network were subject to unchanging sensory drive, the network would be forced to adopt a new stable state (until removal of the stimulus).

In the case of the putative multi-bump GC attractor network, the hexagonal pattern represents the global minimum of the system’s energy function and depending on its exact properties can be robust to small perturbations. However, even small but constantly applied perturbations will distort the stable state, since these perturbations become essentially a feature of the system’s dynamics.

The question is then whether the CAN could be forced into a state that resembled a sheared pattern. Although a mathematical proof is not provided for this specific network, results from related domains suggest this possibility. In the problem of circle packing, a square packing is a close second to hexagonal packing (packing density 78.5% and 90.7% respectively in Fig. 3.1G). In neuroscience domains, it has been observed (Dordek et al. (2015a); Stachenfeld et al. (2014)) that the principal components of the transition structure of an environment often converge to square rather than hexagonal lattice configurations, suggesting that the latter is sometimes informationally or energetically preferable.

The key insight is to realize that square and hexagonal lattices are closely related by a simple shearing transformation. In essence, the square to hexagonal lattice transformation is one that preserves the organization of the nodes. In contrast to a random organization of nodes, the difference between the two configurations is clearly more energetically related. However, just as in a mesh of nodes connected elastically, the shearing requires the length of the edges to change, introducing tension into the system which will act to return it to its optimal configuration. However, if the tension in the edges is too great, the stable equilibrium can be reduced to noisy instability.

The first part of this chapter thus aims to explore whether a multi-bump static hexagonal pattern can be deformed by strong sensory stimulation, such that it is forced to adopt a new, sheared pattern. The initial analyses in the following sections make some important simplifying assumptions. Firstly, PI of the activity pattern is not considered, instead it is only considered whether the static pattern might be
distorted. This assumption implicitly assumes that the animal is stationary, which may have implications for the form of the stimulation profiles applied (this will be discussed in more detail during discussion of the simulation results). Thirdly, sensory drive to the GC sheet is provided by either BVCs or PCs and assumed to be mediated by synaptic associations. These associations are, unless otherwise stated, assumed to be pre-learned.

Lastly, the proposed mechanism incorporates the finding that GC firing patterns are known to initially expand upon first exposure to an environment, before gradually contracting over time [Barry et al. (2012)]. In the following simulations, this contraction is combined with the sensory drive, forcing the grid scale to distort as it attempts to maintain both its sensory associations and its intrinsically optimal configuration, given the firing patterns. The reader is referred to Fig. 3.3B&C for an illustration of this mechanism.

### 3.2.1 Dynamic contraction with stimulation from BVCs

Firstly, simulations assumed BVC drive from four BVCs, each responding to one wall of a square box. The BVC model of chapter 1 was used, with $\alpha$ (the rate of decay / drop-off in firing from the wall) set to $\alpha = 5$. Simulations considered a range of scale ratios while also varying the strength of the BVC input. In each simulation, the grid pattern was allowed first to spontaneously develop at a scale ratio of $X/\lambda = 2$, before being gradually contracted in small increments to a final scale ratio of $X/\lambda = 6$.

A multi-bump attractor pattern was simulated on a square sheet with connectivity fading radially, where the ‘walls’ of the environment (the horizontal and vertical edges defined by the BVC firing) described a a smaller square within the enclosing sheet (Fig. 3.2B, C).

Firstly, in absence of stimulation the grid pattern showed a uniform distribution of alignment values relative to the orientation of the BVC fields, regardless of the grid scale, but even weak BVC stimulation was sufficient to induce alignment (~10% of maximum membrane voltage). At integer scale ratios, the grid pattern tended to align exactly to one of the perpendicular walls. However, non-integer scales caused the GC system to distort in some cases (3.2C) and totally prevented the formation of a stable pattern in others.

Next simulations examined the form of the static pattern following a gradual contraction from an initially stable state. As predicted, as the strength of the stimulation increased the static pattern was forced away from its energetically optimal hexagonal form (3.2). However, the distorted patterns could not be easily described by a shearing process; rather, the BVC stimulation tended to drive the GC pattern in between the fields causing the pattern to be largely abolished. Moreover, the value of $A_{\text{min}}$ (the smallest alignment of either of the grid axes to either the N-S
Fig. 3.2: **A** Dynamics contraction of the CAN with fixed inputs from 4xBVCs at each of the walls. $A_{\text{min}}$ is the minimum angle of the three grid axes to one of the walls (red-dashed lines). $X/\lambda$ is the *box-scale* ratio, where $X$ and $\lambda$ are the box size and grid scale, respectively. $G_{60}$ is the gridness score (see chapter 2). $B$ is the BVC strength, expressed as a proportion of the maximal firing rate across the sheet. Each subplot represents the same contraction experiment at different values of BVC stimulation strength, normalised to the peak firing rate of the CAN sheet. **B** An illustration of the contraction of the grid, BVC strength = 0.1, Red lines denote the locations of the BVC input. **C** Example of distorted pattern produced by large BVC drive.

or E-W directions defined by the BVCs) tended to stay fixed near to $0^\circ$ (Fig. 3.2A; top row), although with transient jumps at higher BVC stimulation. These jumps correspond to transitions in the scale of the grid pattern (3.2A; middle row). Unlike when directly optimizing scale in the previous chapter, changes in scale tended to oscillate between discrete values in a non-monotonic fashion (3.2).

### 3.2.2 Dynamic contraction with stimulation from PCs

The previous chapter discussed the possibility that PCs might provide strong stimulation to GCs in the corners of an environment. In addition to a concomitant contraction in scale, this anchoring might drive distortions in the grid pattern that would manifest with increasing experience ([Stensola et al., 2015]). This stimulation might perhaps reflect strong associations formed by animal trajectories that over-represent the corners, or an increased density or firing rate of the PCs in the
corners reflecting the saliency or relatively low perceptual ambiguity (as opposed to featureless edges, for example).

An identical simulation that presented in the previous section was therefore conducted, with the exception that PCs, rather than BVCs, were assumed to drive the GC sheet. Motivated by the hypothesis proposed above, two PCs were simulated in diametrically opposing corners of the inner square region of the GC sheet (3.3C).

Again, the grid pattern was initially allowed to settle to a stable configuration before gradually contracting its scale.

Intriguingly, whereas the stimulation from the BVCs prevented the pattern from remaining grid-like, a drive from two PCs allowed the attractor pattern to stably distort (Fig. 3.3B), as if by a shearing-like transformation. Importantly, at higher levels of stimulation, the distortion was great enough that $A_{\min}$ consistently and stably remained around $7.5^\circ$ for large periods of scaling. This mechanism, unlike the BVC stimulation, seemed to suggest that such a contraction might be stably supported, making it more likely that it would support the experimentally observed phenomenon over a large range of grid scales.
3.2.3 Mapping to biological learning

The results demonstrate that a CAN is capable of sustaining sheared but grid-like patterns. Stimulation by BVCs, while capable of distorting the grid pattern, did so at the expense of maintaining the base grid pattern. In contrast, stimulation by a pair of PCs at diametrically opposing corners encouraged the grid fields to coincide with the stimulation without stimulating cells which would otherwise be inactive (Fig. 3.3B). By forcing some of the grid fields to overlap at a certain distance while also contracting the preferred (intrinsic) scale, an exact shearing transformation was produced.

However, it is important to emphasize that these results do not represent a full mechanistic interpretation of how the grid pattern readout would be distorted; rather, distortion of the static multi-bump pattern is taken as an initial proxy for the full scenario, which would require translating the grid sheet pattern with the animal’s movement in real space.

Stimulating the sheet makes the implicit assumption that the PCs providing the stimulation have developed synaptic connections to a specific set of GCs. This is a reasonable assumption given the initial configuration of the GCs in novel environments, which might arise from Hebbian learning. The second assumption was that following initial learning, the learning rate was set to zero as the intrinsic scale was contracted (alternatively, the scale contraction happened over a much faster timescale than Hebbian learning). Thus, the observed effects are a simulation of pre-learned but fixed associations under a contracting intrinsic scale. This mechanism neatly combines two experimentally observed phenomena discussed earlier, namely that the shearing can be described by the interaction of fixed pre-learned associations to the corners of an environment \cite{Stensola et al. (2015)} combined with experience-dependent re-contraction in scale \cite{Barry et al. (2012)}.

Lastly, although it is difficult to define an exact correspondence between these results and those presented in the previous chapter, the concept of overlap is relevant here; stimulating the GC sheet explicitly encouraging the activity on the grid sheet to align with the sensory stimulation. Thus, the results can be viewed in terms of maximizing overlap for the GCs population, with the caveat of additional ‘energy’ contained in the system in the interaction between GCs, which was not considered previously.

3.2.4 Dynamic contraction with stimulation from learned GC pattern

Translating the results to the readout

Although stimulation in two corners of the sheet was motivated loosely by experimental observations \cite{Stensola et al. (2015)}, translating these results to real-world
Fig. 3.4: Dynamic contraction with stimulation mirroring the initial firing of the GC sheet, $P = 0.25$. A Change in the scale of the activity pattern following a contraction of the intrinsic scale is minimal, indicating that the grid is strongly driven by the original firing pattern. Each line corresponds to a single contraction trial starting at initial scale ratio $x/\lambda_0$. B Changes in orientation are minimal. C Examples of activity pattern with stimulation by the initial pattern. When stimulation is low, the grid pattern contracts with the intrinsic scale ratio (although slightly less, see A) but preserves the shape (does not distort or realign). When stimulation is high, the grid is fixed even under the intrinsic contraction. Unlike in previous simulations, there was no region of stimulation strength that caused strong deformation of the pattern.

firing patterns requires a consideration of the relationship between the static attractor pattern and the full readout grid pattern resulting from PI. Under the assumption of perfect PI with a chosen grid scale, as long as the size of the CAN sheet is large enough the environment may be mapped directly from real space to an equivalent representation in grid space. That is to say, if the animal explores a square environment, only a square region of the CAN sheet will ever be active.

The static pattern assumption considers the case where the animal is at a specific location. Thus, it is assumed that the PCs active at the corner in fact project to two distinct locations on the grid sheet. This situation could arise in the multi-bump case, since both areas of the sheet would be active at the same time, stimulating Hebbian learning to both locations. However, Hebbian learning would also generate associations with all the other active locations on the other vertices of the hexagonal activity pattern. Thus, a more realistic scenario would be to consider the effect of rescaling given pre-learned stimulation to the sheet in a hexagonal pattern, rather than in two distinct locations.

Results

To test this possibility, a third analysis was conducted which followed a similar paradigm as in the case of the previously defined stimulation patterns. However, rather than define an arbitrary stimulation pattern on the GC sheet, the stimulation pattern was taken as the initial stable grid pattern, approximating a Hebbian learning process while the animal remained at a fixed location (Fig. 3.4C). The intrinsic grid scale was contracted gradually from $100 - 70\%$ of its intrinsic scale.
Stimulation by the ‘learned’ grid pattern did not produce the same systematic distortion patterns as observed in the simpler two-corner stimulation, regardless of grid scale (Fig. 3.4A). Instead, the grid pattern tended either to ignore or be dominated by the stimulation at low and high input strengths, respectively (Fig. 3.4C). The transition in behaviour was sharply marked, although intermediate levels of stimulation did produce an intermediate solution in the static pattern at large contractions (Fig. 3.4. However, the distortion was not significant enough to produce systematic orientation offsets (Fig. 3.4B).

3.2.5 Intermediate summary

In summary, although it is possible to distort the static attractor pattern on the grid cell sheet, it is unlikely that the stimulation pattern needed to do so would arise from Hebbian learning processes in a multi-bump solution. Moreover, in order to continuously shear the pattern the stimulation profile would need also to shift along with the pattern.

Although it is possible that such a sheared pattern could be translated on the sheet in the case of a system performing PI using the shifter mechanism of Burak and Fiete (2009), which is agnostic to the shape of the pattern, taken together the analyses presented thus far suggest that it is unlikely to be the mechanism underlying the shearing of the grid pattern described by Stensola et al. (2015).

A second interpretation of the simultaneous two corner stimulation modelled earlier would be to assume a single-bump configuration with distinct inputs at each corner of the sheet driven respectively when the animal was at either of two corners in the real environment. In this case, simultaneous stimulation could be considered a temporal average of the two distinct inputs, which occur in two different positions. In this case, the shearing would result from both stimuli ‘pulling’ the activity bump as a function of distance to each of the stimulation locations, such that the distortion is a result of a ‘smearing’ of an unperturbed base pattern rather than the perfect translation of a distorted pattern.

However, the correspondence relies on assumptions about the nature of the interaction between the corrective sensory input and the attractor dynamics and the timescale across which those dynamics evolve. This latter hypothesis is the subject of the next section.

3.3 Distortions in a CAN performing PI

So far, simulations have considered distortions to the static grid pattern of a multi-bump CAN as a proxy for the those observed in experimental firing rate maps, which are generated by plotting spikes from individual cells against the location at which they were recorded. In this section, the analyses is extended to investigate whether
shearing might arise as the temporal average of stimulation to a single-bump CAN applied in two diametrically opposing corners of a given environment.

To implement PI a previously published mechanism was adapted, which uses a cell-centered asymmetric connectivity matrix (Fig. 3.5B; Zhang (1996)) to translate the current activity pattern. This asymmetric matrix is the directional derivative of the stationary weight profile in the direction of movement (Fig. 3.5A), allowing the pattern to be preserved perfectly during translation. The speed and heading direction of the animal modulate the magnitude and unit vector direction of the asymmetric component, translating the pattern linearly with movement in real-space. The weight matrix $W$ in eq. 3.1 then becomes:

$$W = W_{SYM} + \alpha \frac{dW}{d\theta}$$  \hspace{1cm} (3.7)

Since the asymmetric component is derived from the static connectivity scheme, translation will necessarily induce further distortions to any distorted pattern, likely leading to imperfect PI. However, the recurrent dynamics should counteract the effects of the distortion such that the pattern remains stable. This is the basis of other PI mechanisms (Burak and Fiete (2009)), which effectively ‘lead’ the pattern to be translated about the sheet by stimulating with a single bump of activity at the current location of activity, but at a slight offset in the direction of motion\(^1\). It is also not implausible that if such recurrent connectivity were learned in the first place, short-term plasticity might mediate an adaptation to the currently deformed activity pattern that would facilitate more accurate PI, although such a mechanism has not been explicitly modelled.

### 3.3.1 Managing drift in path integration

The system was first tested in its ability to perform PI with an undistorted grid pattern. To perfectly translate the static pattern, the timescale of the recurrent attractor dynamics must be large in comparison to the timescale of movement, as the former are then able to correct small movement-induced distortions. However, even when running the simulations at a high temporal resolution, it is impossible to completely eliminate drift in the attractor pattern (Fig. 3.5B,C).

Interestingly, imperfect shifting of the attractor pattern would produce an asymmetric GC field, skewed in the direction of movement (Fig. 3.5C, right). Thus, the firing rate would increase ‘in anticipation’ of reaching the COM of the actual GC field location. Were the animal to only visit the GC field from one direction at one velocity, the skewed shapes in Fig. 3.5C would be perfectly transcribed into real space, however under a random walk policy the field would be entered

\(^1\) A neural ‘carrot on a stick’.
Fig. 3.5: **A** The symmetric and asymmetric connectivity matrices as defined in [Zhang (1996)](). **B** Drift in the grid pattern over successive periods. Each panel shows the firing rate map produced from plotting the activity of a specific cell on the grid cell sheet vs. the position of the agent in space. Compare the location of the leftmost fields in the leftmost panel to the same fields in the other panels. **C** (Right) Timescale of recurrent dynamics must be larger than the timescale of movement to correct distortions to the grid pattern. (Left) 1D simulation of the connectivity profiles in **A**.
from an approximately uniform distribution of locations over a range of velocities. Thus, the firing field would represent an average of all these entries, resulting in an approximately symmetrical field shape. It might therefore be expected that near boundaries, where it is impossible for the agent to enter the GC field (or in fact, PC field) from the boundary direction, those fields might be skewed away from the boundary.

### 3.3.2 Reset by sensory cells

Existing GC models eliminate drift by providing a resetting stimulus at specific locations in the environment, mediated either by PCs or BVCs (Guanella et al. (2007b); Burak and Fiete (2009); Pastoll et al. (2013); Hardcastle et al. (2015)). It has been demonstrated that error in real grid firing fields increases with time and distance since boundary encounters (Hardcastle et al. (2015)). Given that cumulative error (and therefore drift) is an inherent property of path integration in GCs, this process could incorporate environmental information to perform sensory reset.

Corrective stimulation in the case of BVCs is illustrated in Fig. 3.6. Each time the agent approaches a boundary the firing of the associated BVC would provides excitatory input to the GC according to BVC-GC sensory associations. In existing models, these sensory associations are assumed to have been pre-learned under low noise conditions such that stimulation is always corrective. If the GC firing pattern has drifted, the erroneously firing GCs would be inhibited, and the correct GCs would be excited, effectively reinstating the correct firing pattern.
Fig. 3.7: A Grid pattern is unstable when relying on pure path integration but stabilized with corrective input from BVC-GC connections. B Contraction of the grid scale beginning from a stable state (left) with fixed BVC-GC inputs. Percentage values represent the contracted scale as a proportion of the original scale $\lambda/\lambda_0$.

### 3.3.3 Contraction of the intrinsic scale with pre-learned PC associations

The proposed model considered two PCs in opposing corners as providing both a corrective and potentially distortive stimulation, however the mechanism is identical to that described earlier in the context of BVCs. As a first pass, the connections between the PCs and GCs are assumed to be pre-learned under noise-free PI (i.e. the perceived and true movement of the agent is identical). Unless otherwise stated, all parameters are the same as those used in [Guanella et al. (2007b)](#). PCs were modelled as symmetrical Gaussian distributions.

Without corrective input, even under zero navigational error the grid pattern eventually drifts over time (Fig. 3.7A, top). In principle, drift could be arbitrarily minimized in silico by decreasing the time-step and increasing the size of the neuron pool, but this would of course not be possible in the biological case. However, as expected when stimulation from two PCs was applied, the readout pattern was stable over arbitrary timescales (Fig. 3.7A, bottom). Simulations suggested that a stable grid pattern was only produced when the variance of the PC receptive fields were small (variance $\sigma_p = 1e - 3$). At larger values, the PCs tended to cause a ‘sticking’ of the grid pattern since PCs fire over too large an area, preventing the pattern from being translated by PI away from either of the corners.

Having confirmed that the stimulation was sufficient to provide ample stimulation to correct for errors in PI, the next simulation asked whether contracting the intrinsic grid scale while maintaining the same corrective input would result in time-averaged distortions.
Simulation results show this to not be the case. Although there was ‘smearing’ of the time-averaged readout pattern, the result was not in line with the experimentally observed distortions (Stensola et al. 2015) or previously simulated results. Rather, the smearing amounted to a decreased gridness score without ellipticity or orientation offset (Fig. 3.7B). This effect was a result of the resetting in both corners amounting to a translation rather than distortion of the grid pattern, due to the strong attractor dynamics.

Lastly, it was tested whether a process of contraction with prelearned input in addition to continual Hebbian learning might result in a stable distorted state. PC-GC weights were learned using Oja’s rule:

\[
\frac{dW_{ij}}{dt} = \alpha G_i (P_j - G^2_i W_{ij})
\] (3.8)

where \(G_i\) and \(P_j\) refer to the firing of GC \(i\) and PC \(j\) respectively, \(W_{ij}\) is the weight from PC \(j\) to GC \(i\) and \(\alpha\) is the learning rate. Oja’s rule (Oja 1982b) is a biophysically inspired modification of the Hebbian rule which prevents the unbounded growth of weights by applying multiplicative normalization and was chosen for its implementational simplicity rather than biological plausibility. After an initial stabilization period in which the initial weights were learned (under noise-free PI), the intrinsic grid scale was again contracted, but this time with continual learning in the PC-GC weights.

Again however, the scheme did not produce the desired distortion in the readout pattern (Figure not shown). Setting a small learning rate caused the weights to adapt too slowly, causing the same distortions outlined in Fig. 3.7B. Increasing the learning rate tended either to produce an undistorted grid pattern with contracted scale, or more commonly to an abolished grid pattern.

3.3.4 Intermediate summary

Winner take-all sensory inputs

The process of developing the simulations outlined in the previous section outlined two principal weaknesses with the approach. It is argued firstly that the failure of the system to produce a distorted readout pattern can be attributed to the nature of the sensory stimulation.

Attractor dynamics are characterized by their ‘winner-take all’ nature. That is to say, the dynamics of the system must relax to a stable state unless strong stimulation is applied (as was done in section 3.2.2). In the case of the CAN under study, the attractor state is defined by the recurrent connectivity, which by design enforces a single dominant ‘bump’ of activity which inhibits all other cells. Although this
bump is translation invariant (which enables the PI property), the system does not permit multiple bumps.

Thus, when the sheet is stimulated at a location other than the currently active one (as is the case during sensory reset), the dynamics are forced to adopt the input location, rather than reflecting a ‘half-way’ point between the two. This is true even when the firing rate of the input stimulation decays away from some preferred centre of firing, as is the case of the simulated PCs. At low firing rates, the stimulation is ignored whereas at high firing rates the stimulation overrides the current bump of activity. Moreover, for the purpose of correcting PI errors in simple systems, this is intuitively a desirable property.

However, it is clear that such a system can not produce a time-averaged distortion in the readout pattern. Such an effect might be plausible if the timescale of the recurrent dynamics were slower such that a perturbation might cause a distortion that took longer to correct. However, as was made clear in initial simulations; fast-timescale attractor dynamics are precisely the property that allow the system to maintain stability, enabling effective PI. Moreover, it is unlikely that such slow timescale dynamics would be biologically realistic. Taken together, this analysis suggests that a mechanism of ‘hard-resetting’ - corrective stimulation of GCs in a CAN, cannot produce the characteristic distortions described by Stensola et al. (2015).

Hard-resetting as a mechanism for learning in novel environments

The analysis also highlights a more general problem with ‘hard-resetting’ models of sensory input. Consider the case where a CAN model is exposed to a novel environment, where all associations are zero. At the starting point, the currently active GCs will learn associations with the currently active sensory cells providing input (putatively PCs or BVCs).

When the animal moves to the next location, one of two things may happen. Firstly, the associations learned at the last timestep may stimulate the pattern corresponding to the starting location, since the sensory cells do not only fire at a point location, instead firing more or less dependent on their proximity to their maximum firing position. This stimulation would interfere with the PI, causing the animal position and actual grid location to fall out of phase.

It might be possible to introduce some gating mechanism, or set the learning rate so low that the PI signal overrides the BVC input while the animal is still exploring. However, the associations that will be learned would then correspond to the erroneous PI estimate, which would accumulate errors even faster in the presence of this weak sensory input. Upon returning to a location already visited, the currently
active sensory cells and GCs will conflict such that no consistent associations can be learned.

The analysis highlights the simultaneous localization and mapping problem (SLAM) and will be discussed in more detail in the following chapters. With the aim of performing SLAM, the current approach bares some similarity to that of RatSLAM (Milford et al. (2004)). However, the principal aim of this work was to explicitly induce distortions rather than produce a perfect mapping. In their system, the authors reduce the inhibition levels such that multiple bumps of activity can compete on the attractor sheet, finding that the system can produce consistent maps of an environment over time. However, the current problem is different, in that the distortions induced are putatively the result of inconsistencies between sensory and PI inputs. Thus, a ‘successful’ solution to the SLAM problem would be to re-learn the sensory associations to adapt to the new environment such as to produce a stable readout pattern. This re-learning was observed in the simulated system, but did not produce distortions.

### 3.4 Conclusion

In this chapter, it was briefly explored whether distortions to the static activity of a multi-bump CAN could reproduce the elliptical distortions and accompanying orientation offsets observed experimentally (Stensola et al. (2015); Krupic et al. (2015)). Qualitatively, it was shown that by pinning the grid fields (by providing strong stimulation from pre-learned PC inputs) while simultaneously contracting the intrinsic scale, the base pattern is transformed as if by a shearing like process. However, these simulations were a reduction of the full problem, since the static (non-moving) grid pattern was adopted as a proxy for the spatially periodic firing patterns that would be observed by plotting the spikes from a particular cell against the position of the animal in space. To do this, a PI mechanism was added to the model, so as to test whether a distorted base attractor could still perform accurate PI. Firstly, it was found that stabilizing sensory inputs were required to prevent noise in the PI from distorting the grid readout. Secondly, it was found that when the intrinsic scale of the attractor connectivity was contracted, the originally stable pattern was abolished due to the conflicting PC and GC stimulation.

In order to remedy this problem, continual learning in the PC-GC associations was allowed such that upon contraction, the GC-BVC associations might adapt to a new stable configuration. However, stable solutions did not produce a sheared or distorted grid pattern, instead producing a blurred pattern with low gridness score that could be described by two superimposed but offset versions of the intrinsic pattern.
It is hypothesized that this inability stems exactly from the winner-take all dynamics of CAN models, which model sensory input as stimulation that is either ignored by or fully rests the current activity pattern, dependent on the relative strength of stimulation and the time over which it is applied. Initial simulations also suggested that such a mechanism might impeded effective learning of the PC-GC associations in novel environments, a crucial prerequisite for the simulations conducted so far.

In the next chapter, the investigation therefore moves away from CANs, exploring whether implementing a more principled mechanism of sensory correction might produce stable distortions to the readout pattern.
4. PROBABILISTIC CUE INTEGRATION: ONLINE LEARNING AND NAVIGATION

4.1 Introduction

An agent navigating in an environment can rely on two sources of spatial information. Firstly, sensory inputs may indicate an absolute position in space. Secondly, PI can be used to compute its current location given known movement from the last known absolute location. GCs are thought to be responsible for performing PI, however navigating based on purely on PI information will eventually lead to drift away from the correct estimate of location. For this reason, current models of grid cells rely on a corrective input from cells that are assumed to convey sensory information about the environment. These cells may be PCs (Fuhs and Touretzky (2006); Pastoll et al. (2013)) or BVCs (Hardcastle et al. (2015)), although PCs are themselves likely driven by BVC inputs (Hartley et al. (2000); Lever et al. (2009a)).

Firstly, these models assume that the corrective input is a ‘hard reset’ such that the stimulus will override the current GC activity. Secondly, the sensory-GC associations via which the corrective stimulus is applied are assumed to have been learned while the agent navigated the environment without PI error.

Typical spatially motivated rodent electrophysiology experiments are conducted in boxes with dimensions ranging from 0.9 – 2.2m². Aside from the space required to set up these environments within a laboratory, the main limiting factor for recording in larger environments is the information rate of spatially related cells in HPC. GCs have low firing rates making it difficult to record sufficient spikes from a sufficient number of fields in large environments so as to be able to determine the properties of the grid pattern within a practical timeframe. Recording from several GCs in a module (Yoon et al. (2013)) can alleviate these issues to some extent, but given the relative sparsity of GC responses in the mEC, localizing and maintaining several recordings from the same module is not always practical. Moreover, this technique assumes that intra-module GCs are correlated exactly.

It is possible that under well-lit conditions (since PI is assumed to be driven in part by visual flow) an agent might reliably navigate a small environment on the basis of PI. However, it is known that even these modest experimental ranges induce drift.
in darkness where there is limited corrective sensory information available, although
tactile cues would still be available at the boundaries.

This latter point raises an important limitation of existing models; sensory input
should clearly not be treated as an ‘all or nothing’ input; in real systems, no in-
formation is perfect and this principle extends to the HPC. In locations away from
borders, geometric information such as the distance or angle to a wall is based on
vision. Rats are known to possess particularly poor vision, leading us to conclude
that the certainty of a given location estimate based purely on vision must decrease
with distance from the boundaries of an environment or other salient visual cues.
Boundary responsive cells (‘border cells’; Solstad et al. (2008)) are likely driven by
whisking and are likely more accurate, but suffer from a short sensitivity range.

Likewise, the reliability of the PI signal should be treated as variable. The PI is
thought to be computed principally as a function of vestibular motion, propriocep-
tion and visual flow. It must then be reasonably assumed that an estimate of PI
made while moving along a surface with perfect traction with walls indicating a
checker pattern would be more accurate than an estimate made when navigating
along rocky terrain in a featureless landscape.1

Thus, rather than sensory inputs always trumping PI estimates, an ideal spatial
navigation would clearly aim to weight these two sources of inputs based on their
relative certainty.

4.1.1 Hard-resetting in novel environments

A hard-resetting scheme amount to more than just inefficiency of data utilization.
Rather, a hard-resetting scheme would prevent a spatial navigation system from
effectively correcting errors. Considering the context of current GC models, if no
pre-learned sensory-GC associations are formed they will need to be learned ‘on
the fly’ during exploration. In this situation, there would be no corrective inputs,
thus accumulated PI errors will mean that where a given sensory-GC pair forms
an association based on their firing when first visiting position \(x\), when the animal
return later a different set of GCs may be active in combination with the same
sensory inputs (assuming sensory inputs to be invariant features of a location in
space).

Under the hard-resetting scheme, upon revisiting a stored landmark (i.e. a location
in space associated ith a particular sensory input), the current estimate of location
would be reinstatituted to the perceived location where that landmark was originally
encountered. Thus, initial landmark encoding will permanently store errors. This
would prevent the animal from correcting these errors over successive visits.

1 Or, in the case of the Morris water maze, while swimming.
Fig. 4.1: Conceptual counter-argument to the hard-resetting hypothesis. A mouse takes two independent trajectories, both leading to the same cheese. Following the first trajectory, the mouse encodes the cheese location at the perceived location, corresponding to a noisy estimate of the true trajectory from the start location. Following the second trajectory, the mouse encodes the same cheese at a different location. Under the assumption of noisy navigation from the start location, a good guess for the true cheese’s location would be the mean of the two estimates.

A simple solution to this problem would be to assume that all trajectories from a known starting location incurred unbiased noise in PI (Fig. 4.1). Successive visits to the same location would encode the landmark at the current perceived location. Under the unbiased noise assumption, a sensible strategy to encoding the true location of the landmark would be to compute the mean of all previous estimated locations.

In a ‘soft-resetting’ scheme, successive revisits would generate conflicting sensory inputs, however the mean of the sensory inputs would converge to the true location of the landmark over successive trials. More importantly however, the conflict in sensory inputs would indicate a high variance associated with the estimate, allowing the the system to rely more on PI estimates if those were considered more certain.

4.1.2 Simultaneous localization and mapping

This conceptual example highlights the far more complex underlying difficulty of navigating in novel environment. How does an agent navigate based on noisy PI estimates without corrective sensory inputs, while at the same time form associations to these inputs? This “chicken and egg” problem is well known in the robotics literature as the simultaneous localization and mapping (SLAM) problem, defined as:

“The computational principle of constructing or updating a map of an unknown environment while simultaneously keeping track of an agent’s location within it”.

81
So far, the discussion has mainly considered the ‘localization’ subcomponent of this definition. That is, how to effectively deduce the current location with respect to a fixed ‘map’. However, in reality either subcomponent is meaningless without the other; more information will necessitate the update of the current map estimate and changes to the map will by association cause changes in the current estimate of location.

The SLAM problem will be discussed more fully in the next chapter, which considers augmenting the system developed in the current chapter with the ability to perform offline inference. There is not one universal solution to the SLAM problem. Rather, the complexity of the solution can vary depending on the demands of the navigation task and strategy. Thus, this chapter focusses on a relatively simple but limited solution based on the principle of optimal cue integration. Moreover, it will be demonstrated that even this simple principle makes interesting predictions about experimental data.

4.1.3 Probabilistic integration as a computational principle

Before discussing probabilistic integration in the context of the HPC, it is instructive to first consider the algorithmic solution to the problem in the form of recursive Bayesian estimation (RBE; Fig. 4.2).

The process of RBE assumes that a dynamical system evolves in a two-stage iterative process. Firstly, the current location estimate is updated based on a known movement model. The movement model describes the probability of transitioning to a new location given the previous location and will in general be a function of the current control input.

A simple example of a movement model would be to use Newton’s equations of motion to calculate the position of a ship at the next time step, given current velocity and acceleration. Importantly, the movement model might be probabilistic so as to incorporate noise in the environment such as the unknown effect of wave forces on the ship’s hull. The control input in this case might be the known angle of the rudder or engine force.

Since RBE is a probabilistic process, the update step considers all transition possibilities. In a continuous domain, this amounts to an integral of all possible transitions from possible previous locations to new (marginalizing over the prior location). In a discrete domain the movement model is equivalent to the transition matrix as used in a Markov decision process (MDP).

Secondly, the measurement step refines the apriori estimate of location at the end of the movement update step with sensory observations. The update is performed by simply taking the product of the updated distribution and the observation dis-
Fig. 4.2: Recursive Bayesian estimation (Wikipedia). A probability distribution describing the posterior belief over the state at iteration $k - 1$ is updated according to the movement model before being corrected by current sensory observations (measurements in the update step). This refined distribution is the posterior distribution for the next cycle.

When used to model systems with Gaussian noise and linear transition functions, RBE reduces to a Kalman filter (KF). The KF will be discussed in more detail in the following chapter in the context of KF-SLAM, however the efficiencies of the KF outline an important computational difficulty associated with RBE. The essence of the KF is its ability to perform RBE without explicitly computing with full distributions, instead making use of the convenient algebraic properties of Gaussian functions to reduce the problem to inexpensive operations on the mean and covariances of the system. In naive RBE, the state space grows to the power of the dimensionality, quickly making practical implementation intractable. Other methods such as particle filtering overcome this problem by approximating the full distribution by sparse sampling.

However, the repeating hexagonal firing patterns of GC can be interpreted as representing a probability distribution over a finite domain. This finite domain is represented by a hexagon centered around each firing field, known as the Voronoi region. In contrast to real space, this ‘grid space’ does not suffer from the problem of representation. This work proposes that a putative GC sheet could represent a discretization of this finite space, with each cell in the sheet encoding the system’s estimate of the true location of the animal occupying that location in GC space through its firing rate. The true location in ‘real space’ is then encoded by the combined estimates of location across multiple scale modules of grid cells, which can be
computed via numerous methods (Mathis et al. (2015); Bush et al. (2015)).

4.1.4 Probabilistic integration as a biological principle

Stating principles of optimality does not imply that the brain necessarily solves problems in this fashion (Bowers and Davis (2012)). In real systems, optimal solutions are often difficult to find when the problems are complex. Moreover, there may be constraints imposed by the resources of the system performing inference such that the ‘optimality criterion’ may not be purely informational. Nonetheless, there are several studies that show that under certain circumstances, the brain may well be striving for optimal ideals (Pouget et al. (2013)).

Probabilistic integration on a behavioural level

Exploring these ideas in a behavioural context, one study (Ernst and Banks (2002)) asked subjects to estimate the width of a floating bar by touch, vision or both modalities. The experimenters first assessed the variance in the haptic and visual estimates independently, then used the inferred variances to predict the combined visual-haptic estimate. The authors found compelling evidence to suggest that the posterior visual-haptic distribution was formed by probabilistically integrating the two sources of information.

Another study (Alais and Burr (2004)) asked subjects to estimate the location of either a visual or auditory stimulus. Visual stimuli were presented as brief ‘light blobs’ projected on to a screen at a controlled angle in front of the subject. The position of brief sound ‘clicks’ was controlled by the interaural time difference of the same stimuli played through two speakers at either edge of the screen. Following the presentation of two stimuli separated by a brief delay, subjects were asked to indicate which stimulus was most leftward. Each stimulus was either unimodal (visual or auditory) or bimodal (both). By varying the ‘blurriness’ of the visual blob, the authors concluded that localization was best explained by a model of optimal integration based on the relative reliability of each sensory stimulus.

Probabilistic integration in neurons

How could these probabilistic computations be carried out in the brain? Several studies have approached this question from the perspective of basic computations and representations at the neural level. Firstly, in order to perform probabilistic computation, the brain must have a way of representing probability distributions (Pouget et al. (2013)). Several studies have argued that neuronal activity might reflect the probability or log-probability of a particular stimulus being present in the neuron’s receptive field (Barlow (1969); Koechlin et al. (1999)).

While the difference between encoding the probability or log-probability might seem trivial, the two schemes might theoretically underlie two separate but equally impor-
tant forms of computation. Computing the products of distributions is the bread and butter of probabilistic computations, but multiplication is not a feature normally associated with synaptic integration. However, by encoding log-probabilities, multiplications are converted to summations.

In contrast, summation of probabilities is essential for performing marginalization or normalization. In the former, the ‘marginal’ distribution of a given variable is computed by ‘integrating out’ the possible values of its conditional dependencies. In normalization, a variable’s distribution is forced to integrate to unity by dividing by the weighted sum of its possible values. Interestingly, divisive normalization exists in many neural circuits (Beck et al. (2011); Ma et al. (2011)) and such computations bear striking resemblance to network level recurrent inhibition and excitation.

Probabilistic navigation

What evidence is there to suggest that navigation involves probabilistic computations? One study asked subjects to navigate to the location of a remembered stimulus by either proprioceptive (PI), visual cues or both. The authors showed that when the two modalities were in conflict, visual cues could either reset or be integrated with PI information (Nardini et al. (2008)). Interestingly, although response variance was reduced when both modalities were available in adults, the same was not true for the 4-5 or 7-8 year old groups, suggesting that navigating by cue integration might be a learned principle. However, if PCs, GCs and the other associated spatially modulated cells in the HPC formation and surrounding areas are indeed important for navigation on a behavioural level, one might expect to see evidence of these probabilistic principles on a neural level.

A meta-study (Madl et al. (2014)) of three published studies examining PCs on linear and circular tracks showed that the place field width was smaller nearer objects on the track, as might be expected if the objects provided exact information about location and the tuning widths of PCs reflected the probability of being at those locations. They also argue that the expansion of place fields in novel environments (Barry et al. (2012)) may reflect increased uncertainty about current location.

The same principle should also apply to place fields away from boundaries; since distance judgement (Yoshioka (1929)) and PI (Hardcastle et al. (2015)) errors increase with distance, the locational certainty should be reflected in the firing fields of PCs.

These observations are present in BVCs (Lever et al. (2009b)) and reflected in the BVC model (Hartley et al. (2000)), where the width of the receptive fields is observed to increase with allocentric distance from boundaries. Surprisingly, it is not clear whether this is the case for place fields. To my knowledge, no direct test of the relationship between place field size and distance to environmental boundaries...
Fig. 4.3: **A** (Top) Subjects were asked to estimate the width of a bar based on touch and vision. In the experiment, the bar was represented by a set of dots floating above the background. Dots appeared at different depths with a mean equal to the mean depth of the background. The variance of the dot depth could be controlled to modulate the reliability of the visual input ([Ernst and Banks (2002)]). (Bottom) Estimates of width were accurately predicted by a model of Bayesian integration, where the larger variance in the haptic estimate (red line) meant that the posterior estimate (green line) relied more on the more certain visual estimate (blue line; [Pouget et al. (2013)]). **B** Outbound and inbound shifts in place fields ([Gothard et al. (1996)]). A slope of 1 indicates anchoring to the box whereas a slope of 0 indicates anchoring to external cues. **C** Grid cells respond more to movement gain that place cells, which are anchored to the visual features of the environment ([Chen et al. (2018)], but see also [Campbell et al. (2018)]).
in open fields exists. However, the same meta-study \cite{Madl2014} demonstrated that while a Bayesian model could predict some of the variance in place field widths on circular tracks as a function of distance from walls and objects, significant variance remained unaccounted for. This finding suggests that receptive fields may not purely represent the probability of their associated stimuli (location), mirroring similar invariance in width of tuning curves in primary visual cortex to orientation stimuli of varying contrast \cite{Anderson2000}. Answering this hypothesis concretely may require recording place fields in larger environments with specifically designed experimental protocols, where the putative effect of PI and visual distance errors would be magnified.

Despite a lack of clear evidence that place fields explicitly represent uncertainty, several studies have shown that place fields integrate several sources of information to determine their preferred centre of firing. In one study, rats shuttled between a starting box and a fixed goal at the end of a linear track \cite{Gothard1996}. During outbound runs (box to goal) the location of the start box was shifted, such that on inbound runs the distance that the animal ran was changed. The authors examined the locations of the observed place fields on the basis of their distances relative to fixed external (goal location) and variable (box) cues. On outbound runs, place fields within 50cm of the box adhered to the box location. Since the animals were running away from the box, this implied a reliance on PI over external cues. However, PCs at the end of the track fired at an unchanged distance with respect to the fixed goal location. Moreover, the transition from box to goal anchoring was a linear function of distance along the track (Fig. 4.3B). Interestingly, on inbound runs, the effect was even more pronounced, with place field locations being determined by PI from the goal location (behind the rat) until 10-15cm away from the start box. This effect may represent the fact that unlike the start box, the goal location was always consistent with external room cues.

A recent study showed that PCs are more strongly anchored by landmarks in deep than in superficial CA1 \cite{Geiller2017}, although this result may reflect increased reliance on non-geometric sensory cues. However, the question as to the degree of reliance on environmental vs. PI cues is also relevant to the firing properties of GCs, especially given the evidence of bidirectional influence between the two cell types \cite{Evans2016}.

A recent unpublished study from our lab \cite{Chen2018} suggests that PCs and GCs are both influenced by PI and visual information, but to differing degrees. By changing the movement gain in a virtual reality (VR) environment, the authors were able to show that GCs relied more on PI cues whereas PCs were more strongly anchored to boundaries. Interestingly, the partial influence of visual cues was stronger when gain was increased (more visual flow but distance moved on a
A styrofoam ball, a finding reported by another study (Campbell et al. (2018)).

4.1.5 Cue integration in current models of grid cells

As discussed in the introductory chapter of this thesis, almost all existing models of GCs are limited in that they typically focus on a single putative feature. The sole exception is the work of Cheung (Cheung (2016)).

Cheung recently proposed a novel system for performing probabilistic integration in GCs capable of reproducing several experimental findings. In his implementation, GCs are assumed to integrate self-motion information with geometric information from the environment, mediated by BVCs. Notably, the system was capable of learning stable associations while navigating with noise in novel environments, rescaling in response to environmental rescaling and showed fragmentation in a hairpin maze.

The system is based on an adaptation of a concept from the robotics literature known as a particle filter (PF). In a PF, the full probability distribution is approximated by a finite set of ‘particles’, where each particle represents a single hypothesis about the current state and maintains its own map.

Unlike in RBE, the movement and measurement updates in a PF have different functions. Rather than updating the full distribution, each particle is updated according to the transition function (often assuming independent noise). However, rather than being refined by sensory inputs in the measurement step, each particle generates a prediction about the sensory input given its own hypothesis about the current state and map, which is compared against the actual sensory input in order to guide a ‘resampling’ process.

In the resampling process, the existing particles are replaced by a set of new particles whose state and map hypotheses are sampled from the distribution of existing samples. However, the sampling is weighted according to the agreement of the predicted and observed sensory information at the current timestep such that particles whose predictions were comparatively accurate are overrepresented in the new distribution. Conversely, particles whose predictions contrast to the true current sensory input are likely to be discarded. In each re-sampling stage, the total number of particles remains fixed.

In Cheung (2016), a particle is assumed to represent a single GC within a module and has associated with it a cell-specific hypothesis about the current location and heading direction of the animal, in addition to a set of weights to a population of ‘predictive boundary cells’.

Despite the predictive power of the system, the resampling stage would clearly be problematic to implement in neural circuitry, since it would require that cells were able to instantaneously change their outgoing weights. In the SI of the paper, the
author notes that the resampling is not strictly a requirement for performing information fusion. However, without resampling the distribution would quickly degenerate since an increasingly small proportion of the particles will maintain accurate state and map hypotheses such that the distribution will become poorly represented, making localization and mapping practically impossible.

A second limitation of the PF approach is that it is based on OI (interference of three oscillators responding to preferred directions within a single cell) to generate the hexagonal GC firing pattern and so does not provide a population level explanation for the behaviour of experimentally observed grid modules (although see Bush and Burgess (2014), which integrates OI models with attractor dynamics). In the study, Cheung shows that the particles display attractor-like dynamics since particles whose spatial phases indicated that they were ‘local pairs’ of GCs (locality was determined by phase matching pairs of GCs) maintained their relative spatial offsets. However, although there would be variation in the spatial phases of the particles since the system is required to track this unknown variable, in reality the distribution of phases would be biased strongly towards the ‘true’ phase (depending on the initial phase offset), contrasting with robust experimental observations of a uniform distribution of phases. Stated another way, in the limit of zero perceptual and movement ambiguity, all GCs (particles) would have the same spatial phase corresponding to the ‘true’ spatial phase of the animal.

Thirdly, although not a limitation of the model per se, the study did not investigate specific experimental circumstances where sensory and PI information might be mismatched. Finally, since the study used BVCs as sensory input to the GCs it made no predictions about the likely reciprocal influence on PC firing.

4.1.6 Outline of approach

In this chapter, a novel mode of GC firing was proposed, wherein PI and sensory cues are integrated according to their certainty based on an adaptation of RBE. It was proposed that the cells in a module represent a periodic discretization of space such that absolute location is represented by combining multiple modules of different scales.

Having considered the deficiency of Cheung’s model in being able to explain the population dynamics of a GC module, it might seem logical to try to implement probabilistic integration in a CAN model. However, attractor dynamics are by definition incompatible with the Bayesian of information integration, since they do not support arbitrary firing pattern across the population. Instead, the distribution would be required to collapse to a predefined form as determined by the recurrent connectivity. Such a configuration would make it difficult to represent complex...
multi-modal distributions (although see [Milford et al. (2004)]).

Although the proposed model does not rely on attractor dynamics, it is however a network level account of GC firing and is inspired in parts by some of the features of existing CAN models. Importantly, it is shown that a network level interpretation naturally reproduces the preserved spatial relationships between GCs that are a feature of attractor dynamics.

Careful attention is paid to biological realism, explicitly discussing how marginalization, normalization and multiplying of distributions could be achieved through neuronal interactions. The resulting model is able to simultaneously navigate while developing associations to sensory cues under low noise conditions. Moreover, it is explored how this process can explain several as yet unexplained experimental observations including experience-dependent shearing and orientation offset and merging of local representations in a global context. It also discussed how the system could support GC driven remapping of PC responses.

The current work focusses on modelling a single grid scale at a time, mostly in the interest of lowering simulation time. However, modelling multiple scales is a topic of ongoing work and is briefly discussed at the end of the chapter. Similarly, the simulations do not explicitly model the head direction signal. Thus, the animal’s ‘state’ simply refers to its $x$ and $y$ position.

4.2 Methods

4.2.1 Representation of space on the GC sheet

Each grid field is repeated over the nodes of a hexagonal lattice [Mathis et al. (2015)]. This lattice can be described by assuming a set of basis vectors $(v_\alpha)_{1 \leq \alpha \leq D}$ in $D$-dimensional space and considering all possible combinations of these vectors and their integer multiples. Each combination points to a node of the lattice:

$$L = \sum_{\alpha=1}^{D} k_\alpha v_\alpha \quad for \quad k_\alpha \in \mathbb{Z}, v_\alpha \in \mathbb{R}^D$$

(matching, the procedure of approximating an arbitrary distribution with another predefined distribution. This procedure is the basis of variational inference (VI), in which simpler families (e.g. exponential or Gaussian) of functions are used to approximate often much more complex distributions by minimizing the Kullbach-Leibler divergence (KL). One study showed that attractor dynamics can be used to perform optimal computations - e.g. computing the position of an object in ego-centered coordinates given its position on the retina and the position of the eyes in the head, given that all are encoded by population activity [Latham et al. (2003)]. However, their analysis was based on fixed tuning distances such that computation cannot be performed on stimuli with varying noise levels, unless the variance is proportional to the amplitude as in the case of Poisson firing statistic. However, it is possible that adaptation to varying noise levels could be mediated by short-term plasticity. Such an augmentation could form the basis of an attractor based Kalman filter, which filters incoming information by applying a time-varying prior belief (the Kalman filter will be explored later in this chapter).
A square lattice would have basis vectors \( v_1 = (1, 0) \) and \( v_2 = (0, 1) \). For hexagonal coordinates, the following basis vectors are used:

\[
\begin{align*}
    v_1 &= [\cos(\phi), \sin(\phi)] \\ v_2 &= [\cos(\phi + \pi/3), \sin(\phi + \pi/3)]
\end{align*}
\]  

(4.2) (4.3)

where \( \phi \) is the rotational offset of the grid lattice (in all simulations, \( \phi = 0 \)). Each lattice point \( p \in \mathbb{L} \) has a domain \( \mathbb{L}_p \subset \mathbb{R}^D \) called the Voronoi region, defined as:

\[
    \mathbb{V}_p = \{ x' \in \mathbb{R}^D | \| x - p \| < \| x' - q \| \forall q \in \mathbb{L} \land p \neq q \}
\]  

(4.4)

i.e. the Voronoi region of \( p \) is that region in which each point is closer to \( p \) than any other point on the lattice. Thus, for any grid field, the Voronoi region defines the base domain in real space.

A position in ‘real space’ is denoted as \( x' \) to distinguish from position in ‘grid space’ \( x \). This notation abstractly assumes that the grid sheet is a continuum, however in reality (and in simulations) this space will be discretized by the finite population of GCs. The function:

\[
v(x') : x' \rightarrow x
\]  

(4.5)

describes the mapping from a position in real space (\( x' \)) to the corresponding position in grid space (\( x \); the ‘wrapping’ function).

The Normal distribution must be interpreted differently over a periodic domain, since any periodic domain is finite. A regular normal distribution defined over this domain would firstly not integrate to one and secondly be discontinuous at the boundaries between the Voronoi regions (Fig. 4.4A). Instead, a periodic (‘wrapped’) Gaussian distribution is defined on the hexagonal lattice (Fig. 4.4C).

A wrapped version of any probability distribution can be constructed by ‘wrapping’ the distribution around the unit circle. In 1D, the wrapped normal distribution is defined as:

\[
    \mathcal{N}_W(x, \mu, \sigma) = \frac{1}{\sigma \sqrt{2\pi}} \sum_{m=-\infty}^{\infty} \exp \left( -\frac{(x - \mu + 2m\lambda)^2}{2\sigma^2} \right)
\]  

(4.6)

In probability theory and directional statistics, a wrapped normal distribution (WND)
is a wrapped probability distribution that results from ‘wrapping’ around the unit circle. The mathematically simpler von Mises distribution closely approximates the WND and has been used to describe grid cells (Mathis et al. (2015)). The von Mises distribution is simply the exponential of a sum of three cosine bands mutually oriented at 120°. However, the notion of covariance is lost in this approximation, so a full WND is preferred is defined for the hexagonal lattice.

The concept of wrapping a probability distribution simply means that at each coordinate, the probability density at that point is the sum of the probability density at that point in addition to the corresponding points in each of the tiled Voronoi domains. For a 1D case this is simple; one is simply adding up the probability density at intervals of the width of the domain up to infinity. The hexagonal case is slightly trickier; one must add the points from each successive ring around the base coordinate (in the first ring there will be 6 points, 12 in the 3rd...see Fig. 4.4B).

4.2.2 The algorithmic level

Recursive Bayesian estimation

RBE is a two step iterative process. Firstly, the movement model is used to update the location distribution from the previous time-step $x_{k-1}$:

$$p(x_k|z_{1:k-1}) = \int_{-\infty}^{\infty} p(x_k|x_{k-1}) \cdot p(x_{k-1}|z_{1:k-1}) dx_{k-1} \quad (4.7)$$

where $z_k$ represents an observation in grid space at timestep $k$. The first term on the right hand side of the equation is the movement model, which expresses the probability of transitioning to a state $x_k$ at the current timestep $k$ given previous location $x_{k-1}$. In a discrete environment with a finite set of states, the movement function would be represented by a transition matrix. As discussed, the transition model is also a function of the known control input $u_k$, however this explicit dependence is omitted for clarity and consistency with the literature.

The second term is the location estimate distribution at the previous timestep. The location estimate is also conditional on the history of previous observations made at each time step $z_k$. The apriori distribution in $4.7$ is then refined by computing its normalized product with the current sensory estimate:

$$p(x_k|z_{1:k}) = \frac{p(z_k|x_k) \cdot p(x_k|z_{1:k-1})}{p(z_k|z_{1:k-1})} \quad (4.8)$$

The first term in the numerator is the measurement model, which is a likelihood function describing the likelihood of making an observation given the current estimate of location. The key feature of the measurement step is that the movement distribution
Fig. 4.4: A The base Voronoi domain of each GC module can be represented by a lattice defined by two vectors defined as in Eq. 4.3 (Mathis and Stemmler, 2015) B The wrapped distribution is constructed by summing multiple periodic points to infinity. Opacity of tiles represents their firing strength based on an unwrapped Gaussian distribution whose mean is at the centre. C (Left) Wrapped and non-wrapped 1D Gaussian distributions. (Middle) The non-wrapped Gaussian distribution confined to the hexagonal Voronoi domains. (Right) The Gaussian distribution wrapped on a hexagonal lattice. D (Left) The posteriori distribution at time $t - 1$. (Middle) The movement distribution is a Gaussian offset by the required distance in the relevant direction. The width of the distribution represents the uncertainty associated with moving the distribution in (Left). A sharp distribution would translate the distribution perfectly whereas a broad distribution adds uncertainty to the resulting distribution (Right).
will be updated to reflect the relative certainties of each distribution. Despite the inherent noise in the sensory observation, the resulting input will nonetheless add information to the system such that the final refined estimate represents the optimal combination of all currently available information. This estimate is typically more accurate that either estimate when considered independently. The normalizing constant:

$$p(z_k|z_{1:k-1}) = \int_{-\infty}^{\infty} p(z_k|x_k) \cdot p(x_k|z_{1:k-1}) dx_k$$  \hspace{1cm} (4.9)$$

simply sums over all possible estimates $z_k$ given the history of previous estimates.

An intuitive example: Non-periodic updating of Gaussian distributions

To gain an intuition for applying RBE to the GC model, it is instructive to first consider the simpler case of updating non-periodic Gaussian shaped distributions. In the prediction step, it is assumed that the PI input can be described by a linear translation proportional to the movement of the animal, with some accompanying Gaussian noise. In the real system, this would account for noise in the updating of the neural system and uncertainty in the estimate of movement given vestibular and visual signals, if both are assumed to be Gaussian. The system update term in eq. 4.7 then becomes:

$$p(x_k|x_{k-1}) = \mathcal{N}(x_k, \hat{u}_k + x_{k-1}, \hat{u}_k^T \Sigma_{PI} \hat{u}_k)$$  \hspace{1cm} (4.10)$$

where the current estimate of movement $\hat{u}_k$ (odometry / vestibular signals) is noisy such that:

$$\hat{u}_k = x_k - x_{k-1} + w_k$$  \hspace{1cm} (4.11)$$

$$\hat{u}_k = u_k + w_k$$  \hspace{1cm} (4.12)$$

where $u_k$ is the true movement at time $k$ and $w_k \sim \mathcal{N}(0, u_k^T \Sigma_{PI} u_k)$ is Gaussian noise with a variance that scales proportionally to the movement magnitude. Using the convolution operation:

$$(f * g)(t) = \int_{-\infty}^{\infty} f(\tau) \cdot g(t - \tau) d\tau$$  \hspace{1cm} (4.13)$$

and substituting eq. 4.10 into eq. 4.7 the computation can be represented as:
The movement update can be intuitively understood as follows. The distribution represents the probability density that the true location of the animal corresponds to the corresponding point in GC space. If the movement update were noise free, the distribution would be shifted, preserving its shape. However, each point in space has a probability of transitioning to every other point in the space. The convolution states that the overall probability of a given location in grid space being occupied is the sum of all possible ways of transitioning to that state, given the previous state. Combining the sensory estimate is then achieved simply by taking the product of this expression with that of the sensory estimate \( z_k \), normalising by the constant in eq. 4.9.

### The movement model

In 2D periodic hexagonal grid space, the wrapped normal distribution is defined as:

\[
N_W(x, \mu, \Sigma) = \frac{1}{2\pi \sqrt{\text{det}(\Sigma)}} \sum_{m,n=-\infty}^{\infty} \exp \left( -\frac{1}{2} (x - \mu + c_{m,n})^T \Sigma^{-1} (x - \mu + c_{m,n}) \right) \tag{4.17}
\]

where \( c_{m,n} = 2\lambda (m\nu_1 + n\nu_2) \), which is an offset that varies with the current lattice point. Note that in the current model noise is uniform in all directions of movement, so \( \Sigma_{PI} \) is in fact a diagonal matrix with the same \( \sigma_{PI} \) at each point along the diagonal.

Using the definition in (4.17), the movement model used as an earlier example in (4.10) is extended to the case where the probability distributions are wrapped within the base GC’s domain in (i.e. the periodic domain outside of which points back to the base domain) \( \mathcal{V}_0 \). Since the GC encoding is periodic, it is necessary to sum over all possible tiling of both the movement distribution and the current distribution:
\[ p(x_k|z_{1:k-1}) = \int_{x_{k-1}}^{x_k} \sum_{m,n=-\infty}^{\infty} \mathcal{N}(x_{k-1} + \hat{u}_k + c_{m,n}, \hat{u}_k \Sigma_{PL}) \cdot p(x_{k-1} + c_{m,n}|z_{1:k-1}) \, dx_{k-1} \quad (4.18) \]

\[ = \int_{x_{k-1}}^{x_k} p(x_{k-1}|z_{1:k-1}) \sum_{m,n=-\infty}^{\infty} \mathcal{N}(x_{k-1} + \hat{u}_k + c_{m,n}, \hat{u}_k \Sigma_{PL}) \, dx_{k-1} \quad (4.19) \]

\[ = p(x_{k-1}|z_{1:k-1}) \ast N_{W}(x_k, \hat{u}_k, \hat{u}_k \Sigma_{PL}) \quad (4.20) \]

Note that an offsetting both distributions produces multiple copies of the same relative offsets, so the tiling needs only to apply over the movement distribution. The term after the summation in eq. 4.20 is simply the wrapped normal distribution described earlier. This also applies in the case of a 2D hexagonal domain.

4.2.3 The implementational level: possible neural mechanisms

The observation model

It is conventional in SLAM to use sensors (e.g. laser or sonar) that return estimates of range and bearing to a given landmark. Assuming that the landmark is uniquely identifiable, these range and bearing measurements can be used either to store the location of the landmark in the map, or retrieve an estimate of the current location. Converting range and bearing measurement to units of location requires a measurement model. More generally, the measurement model \( p(x|z) \) is a function that converts some arbitrary sensory input \( z \) (e.g. neuronal activity from sensory cortices) into a likelihood distribution in grid space \( x \).

PCs are known to fire at defined locations in space. Of course, a ‘location’ in absence of an internal model of that space is simply a unique combination of sensory inputs. Thus, it is assumed in the model that PCs respond to unique combinations of sensory inputs, which themselves are attached to specific positions in space. In the robotics analogy, PCs represent ‘landmarks’ within an environment. Thus, PC firing constitutes the raw sensory input \( z \) and the observation model must convert this firing into an a likelihood function in grid space \( p(x|z) \).

If it is assumed that the receptive fields are radially symmetric and decay with distance, the PC firing rate can be interpreted as a range measurement. In principle, a range measurement is sufficient to determine the current location within an annulus centred on the current landmark, assuming no bearing information. Given range measurements from several landmarks at different locations, the location may then be uniquely determined via triangulation (the unique point where three annuli overlap).

However, the detail of performing such a triangulation on the GC sheet is not immediately clear. If PCs are assumed to have simple connections projecting to the GCs, the PCs can only provide drive via a fixed set of weights, where the strength
Fig. 4.5: A (Left) Tuning (Left) and organization (Middle) of the cricket cercal interneurons. (Right) Error in decoding the true wind speed $s$ (adapted from Miller et al. (1991) and Dayan and Abbott (2001)). B (Top-left) Twisted torus configuration. Path integration along this shape would produce grids arranged on a hexagonal lattice, since each revolution around the larger radius produces a half-rotation around the smaller radius (the ‘twist’). (Bottom-left) Regular torus configuration. Path integration along this shape would produce grids arranged on a rectangular lattice, equivalent to joining the opposite edges of a rectangular piece of paper. (Right) Example distribution represented on the GC sheet. C Shifter cells from Burak and Fiete (2009). Each GC is tuned both to heading direction and velocity, by virtue of connection strengths between different head direction and velocity tuned cells. Each cell has a connectivity matrix that is skewed in the same preferred direction.
of the drive is modulated by the firing rate.

**Bayesian location decoding.** To perform the triangulation described above, the measurement model would need to provide and input to different GCs depending on the current firing rate of the PC. This is the essence of commonly used Bayesian decoding techniques (Brown et al. (1998); Dayan and Abbott (2001)), which typically assume a population of PCs whose receptive fields (which describe their time average firing rates) are described by Gaussian functions:

\[
f_a(x) = r_{\text{max}} \cdot \exp\left(-\frac{1}{2}(\frac{x - x_a}{\sigma_a})^2\right)
\]  

(4.21)

where \(x_a\) is the preferred firing location of PC \(a\) and \(\sigma_a\) is its tuning width. In a single trial (a time of length \(T\) over which a measurement is made), it is possible to approximate the firing rates of each PC as \(r_a = n_a/T\), where \(n_a\) is the number of spikes fired during that period. The probability of observing \(r_a\) given the location \(x\) assuming homogeneous Poisson firing is then given by:

\[
P[r_a|x] = \frac{(f_a(x)T)^{n_a}}{(n_a)!} \exp\left(-f_a(x)T\right)
\]  

(4.22)

The firing rate probability of the population is then obtained by taking the product of all neurons, assuming their firing is independent.

Note that the ‘peakiness’ of the probability distribution for each neuron becomes larger with \(T\), since with a larger sample the probability of observing \(r_a\) becomes increasingly unlikely away from the corresponding location in \(f_a(x)\). Thus, in this scenario the agent would in theory be able to determine its location exactly if it simply waited for a long enough time to reduce the uncertainty in its sample.

**Plausible location decoding** Returning to the biological problem, it is unclear how PCs might drive different GCs according to their firing rates. A possible solution would be to assume a population of sensory cells, such as BVCs that respond to specific combinations of allocentric distance and angle to environmental boundaries (Cheung (2016)).

However, there is strong evidence to suggests that BVCs may drive place cells in this way (Burgess and O’Keefe (1996); Hartley et al. (2000); Lever et al. (2009a)). PCs can thus be viewed as the intermediary that processes the range and bearing measurement from BVCs and converts them to unique positions in space. Thus, a more experimentally plausible solution might be to assume GCs are driven by PCs, rather than by BVCs or direct sensory input.
A weighted drive of place cells does not constitute an optimal decoding solution, since a single PC cannot drive different GCs based on the current location. However, given a finite population of PCs, a weighted input can effectively perform an interpolation between spatial locations represented by each PC. In the limit where the PC population is infinite and their tuning widths infinitesimally narrow, the code will be able to determine the current position exactly, although such a code would be inefficient. However, with a reasonable density of PCs whose receptive fields overlap to some degree, a unique location can be decoded with reasonable accuracy. Thus, in the model it is assumed that an sensory input is interpreted by PCs, whose raw firing rates $P$ are mapped to observations in grid space by some PC-GC weights $W_{PG}$:

$$p(x_k|z_k) = W_{PG}P$$ \hspace{1cm} (4.23)

Thus, although not the optimal solution for converting sensory input into observations, a simple mechanism of weighted PC drive is perhaps more plausible. Moreover, in practice the efficiency of a Bayesian approach over the simpler proposed one is highly dependent on the difficulty of the decoding problem. This is illustrated with an example from the cricket cercal system (Miller et al. (1991); Dayan and Abbott (2001)), which is used by the cricket to infer the direction of air currents. Fig. 4.5A shows the response of four circal interneurons whose preferred wind direction $s$ are organised in $90^\circ$ intervals and whose tuning curves are approximately Gaussian (or cosine) shaped. Using only four neurons, both a weighted average and Bayesian decoding approach produce good estimates of the true wind speeds, with the Bayesian approach performing slightly better.

**The path integration circuit**

To implement the movement update in a biologically plausible way, the proposed mechanism takes advantage of the fact that the convolution of two quantities is equal to the summation of the product of the two quantities, at every possible offset of the second quantity. Since the movement function is a periodic (wrapped) function of all possible cyclic offsets, the convolution in eq. 4.20 can be replaced by a circular convolution with a circulant matrix:

$$N_{Wc} \times G = N_{W} * G$$ \hspace{1cm} (4.24)

where $G$ are the grid cell firing rates. Each row of circulant matrix $N_{Wc}$ is simply the movement distribution $N_{W}$ cyclically shifted by an offset denoting the index of the cell. The description is more difficult to intuit than the physical reality; the resulting matrix simply corresponds to a recurrent weight matrix of dimension...
where each cell has the same local connectivity pattern. In the context of a PI network performing PI, each GC will have a Gaussian shaped connectivity to other cells in the network with mean and variance proportional to the velocity.

However, to perform accurate PI the connectivity would need to adapt to the current velocity and heading direction of the animal. To overcome this, the ‘shifter cell’ mechanism (Burak and Fiete (2009)) is adapted.

In the modified implementation, a separate population of shifter cells which are driven but also back-project to the ‘readout’ population is assumed. The shifter cells are conjunctive (Sargolini (2006)) such that they each have preferred heading directions. The shifter cells have Gaussian tuned back-projections where the Gaussian variance and mean are proportional to a fixed offset distance.

In all simulations, it is assumed that each readout GC has 4 corresponding shifter cells $G_{\theta}^{ij}$, each tuned to one of four principal directions $\theta$ separated by 90°. Each shifter cell fires in proportion to the projection of the current heading velocity vector $v$ on to its preferred firing direction, multiplied by the drive from its corresponding readout cell $i$.

However, so far the network would only allow the current pattern of activity to be translated by a fixed amount in an arbitrary direction but not remain stationary, since the offset connectivity has a fixed offset on the grid sheet. Thus, a fifth corresponding shifter cell type is assumed, $GC_{0}^{ij}$ which back-projects only to the corresponding readout GC. These cells are effectively self-connections, however their firing is independent of heading direction and negatively proportional to the current velocity magnitude. The shifter cell firing is then defined as:

\[
S_{\theta}^{i}(v) = \left[ \frac{v \cdot \hat{e}_{\theta}}{V_{\text{max}}} \right]^{+} \cdot G_{i}, \quad \text{for} \quad \theta = [0^\circ, 90^\circ, 180^\circ, 270^\circ] \quad (4.25)
\]

\[
S_{0}^{i}(v) = \left[ \frac{V_{\text{max}} - |v|}{V_{\text{max}}} \right]^{+} \quad (4.26)
\]

where $[\cdot]^{+}$ is a threshold linear activation, such that two shifter cells with preferred directions 180° apart never fire together. $\hat{e}_{\theta}$ is an normalized unit vector denoting the preferred firing direction of cell $j$. Note that this notation account for both direction and magnitude; the magnitude is scaled as a proportion of the maximum velocity $V_{\text{max}}$, which is assumed to be larger than the maximum velocity of the animal as measured per timestep $\Delta t$. The offset distance of the asymmetric connectivity matrices is also set to $V_{\text{max}}$. The back-projecting weight matrices are:
\[
W_{\theta}(\mathbf{x}_i, \mathbf{x}_j) = N_{W}(\mathbf{x}_i - \mathbf{x}_j, 0, V_{\text{max}} \Sigma_{PL}) \\
W_{0}(\mathbf{x}_i, \mathbf{x}_j) = \delta(\mathbf{x}_i - \mathbf{x}_j)
\]

where \(\mathbf{x}_i\) and \(\mathbf{x}_j\) are the positions of the readout cells in grid space. Thus, as velocity increases the firing rates of the symmetric (static) and asymmetric shifter cells decrease and increase, respectively. Under this scheme, the effective back-projection from the shifter cells to the readout population is a linear interpolation of the current activity (provided by the static self-connecting cells \(S_{ij}^{0}\)) and an asymmetric drive (provided by the asymmetric shifter cells \(S_{ij}^{\theta}\)). Thus, despite the shifter cells having a fixed offset distance, the weighting between the symmetric and asymmetric shifter cells allows an effective back-projection to an arbitrary distance when the velocity is in the range \(|v| \in [0, V_{\text{max}}]|\).

The system can then be modelled as a first order ODE:

\[
\tau \frac{dG_i}{dt} + G_i = S_{ij}^{0}(v) + \sum_j \sum_{\theta=0:90:270} S_{ij}^{\theta}(v) \cdot W_{\theta}(\mathbf{x}_i, \mathbf{x}_j)
\]

where \(G_i\) is the firing rate of GC \(i\). Since the both the outgoing and recurrent weight matrices to the static shifter cells are diagonal matrices with unity weights, the explicit dependence on the weight matrix is dropped to simplify the notation.

The equivalence of the algorithmic and neural implementations of the movement update are illustrated in Fig. 4.5D. As can be seen, the neural mechanism performs identically to the algorithmic solution, tracking not only the mean of the current location (Fig. 4.5D, Left) but the shape of the distribution over time (Fig. 4.5D, Right).

The connectivity defined in the asymmetric connectivity matrices in eq. 4.28 produces 2D periodicity in the PI such that movement past one of the edges of the hexagonally connected sheet continues on the opposite edge (Fig. 4.5B). In the CAN literature, this connectivity scheme is known as a ‘twisted-torus’, which is constructed by joining the opposite edges of a hexagonal sheet. As discussed, the topographical arrangement of GCs on the ‘sheet’ does not necessarily reflect the connectivity, however in all it is assumed for visualization purposes.

An important caveat to this implementation is that it has been assumed that the width of the recurrent connectivity kernels accurately reflects the noise in the PI system. This noise would amount to both noisy estimates of actual movement (so called odometry errors) as a result of processing vestibular / sensory signals, but
also noise in the neural machinery implementing the PI circuit.

Ideally, the real system would also be able to manipulate the width of the recurrent connectivity to adapt dynamically to current estimates of certainty; if the animal were navigating on uncertain ground in the dark, the PI estimate would be less certain. If the movement distribution simply translated the shape perfectly (or as perfectly as possible in a real system), there would be disproportionate weighting of the movement estimate meaning that the estimated state would quickly diverge from the real state.

It is plausible that the mechanism could be modified to account for this possibility, however it was not explicitly modelled. Similarly, it was assumed that the asymmetric weights have been learned beforehand, rather than model this learning process ourselves. It has in fact already been demonstrated that a network capable of performing PI could be learned through an unsupervised Hebbian learning process (Widloski and Fiete (2014b)), although the authors assumed perfect translation of the activity pattern. An interesting line of future work would allow learning of the full network.

The measurement update

In the algorithmic implementation of the measurement update, the _apriori_ distribution following the movement update is multiplied by the current sensory observation to produce the overall refined _aposteriori_ estimate. Although there is some evidence for multiplicative synapses (Koch and Poggio (1992)), neurons are commonly assumed to sum their dendritic inputs. This problem is circumvented by using a logarithmic activation function to the GC and PC populations:

\[
f(x) = \begin{cases} 
\log(x), & x \geq 0 \\
0, & x < 1 
\end{cases}
\]  
(4.30)

i.e a thresholded logarithmic function, since the firing rates must be positive. This imposes the constraint that the measurement and sensory estimates must be > 1 everywhere in order to remain within the operating range of the threshold function. Since there is not constraint that the distributions must sum to 1 at this point, the firing rates could plausibly be scaled to enforce this condition and not affect the integration process.

The final stage of the process would be to perform the reverse logarithm operation, effectively sharpening the distribution. This latter process could plausibly achieved either with exponential-like activation functions or by a circuit with winner-take-all type dynamics, where the cells with the largest firing rates are accentuated and inhibit other cells.
The normalizing circuit

To prevent firing rates from growing unboundedly, the \textit{aposteriori} firing rates (after the measurement update) are normalized such that the network activity sums to 1. This could be simply achieved by adding recurrent inhibition, where all cells in the sheet project to a single interneuron which itself projects back to the grid sheet. In combination with blanket excitation $E$:

$$
\tau \frac{dG}{dt} = -\sum G + E \quad (4.31)
$$

where $G$ are the firing rates of the GCs. Solving the steady state shows that $\sum G = E$, therefore the summed firing rates of the GC sheet can be set to a prescribed value (e.g. 1, for a valid probability distribution).

Learning the PC→GC weights

Discussion to this point has involved the ‘localization’ component of the SLAM problem, which assumes a pre-learned ‘map’. In the context of the proposed model, the cognitive map is represented by the synaptic projections from the PCs to the GCs. Each PC is assumed to have all-to-all connectivity to the GCs sheet (this is not an essential requirement, as will be explored later on). Crucially, the weights from a given PC $W_i$ to the GC sheet encode the distribution representing the estimated location of that PC (landmark) in GC space. Learning is implemented using the BCM rule (Bienenstock et al. (1982)):

$$
\tau_w \frac{dw_{ij}}{dt} = g_j(g_j - \Theta_j)p_i \quad (4.32)
$$

$$
\tau_\Theta \frac{d\Theta_j}{dt} = g_j^2 - \Theta_j \quad (4.33)
$$

where $p_i$ and $g_j$ are the firing rates of the $i^{th}$ and $j^{th}$ PC and GC respectively. $\Theta_j$ is an adaptive threshold specific to each GC that determines whether the PC-GC connection is strengthened or weakened. The threshold tracks the squared value value of its associated GC and has a smaller time constant than the learning rate time constant (typically $\tau_w \approx 10\tau_\Theta$) to ensure that the weights do not grow unboundedly.

This learning rule implements competition between the weights; PC weights to GCs that do not tend to overlap decrease at the expense of projections to GCs which correlate more strongly. The learning rate should reflect the timescale of exploration of the environment such that the weights learn to represent the average, rather than most recent correlations in PC-GC firing.
Importantly, the learning step takes place between the \textit{apriori} GC distribution and the current sensory observation (PC firing). Learning step can thus be viewed as an error correction step between the ‘predicted’ GC firing from the observation model (eq. 4.23) and the ‘true’ GC firing from the sensory inputs. Such a weight update could feasibly be implemented neurally and might result in better performance than the BCM rule, which is only an approximation to this optimization goal.

The choice of the BCM rule was ultimately justified by neural plausibility and simplicity. However, qualitatively similar results were obtained using both the Oja rule (\cite{Oja}) and a delta rule, which simply corrects the squared error between the observation and posterior estimates.

\textit{Final notes}

The complete system architecture is illustrated in Fig. 4.6 and can be summarized by the following algorithm:

\begin{algorithm}
\caption{Online navigation and learning}
\begin{algorithmic}[1]
\State initialize: $W_{P2G} \sim \mathcal{U}(0, 1)$;
\While{$t < T$}
\State do\_movement\_update; \hspace{1cm} \text{Eq. 4.20}
\State make\_observation; \hspace{1cm} \text{Eq. 4.23}
\State update\_PC\_GC\_weights; \hspace{1cm} \text{Eq. 4.33}
\State do\_measurement\_update; \hspace{1cm} \text{Eq. 4.8}
\EndWhile
\end{algorithmic}
\end{algorithm}

Although this chapter also outlined the details of a plausible neural implementation, all simulation results were obtained using the algorithmic implementation for computational efficiency. However, the observation model and learning mechanism are those detailed from the neural implementation.

\subsection{4.3 Results}

\subsubsection{4.3.1 PC \to GC Weights Self-stabilize}

Unless otherwise specified, in all simulations sensory input was mediated by a population of PCs with Gaussian receptive fields. In all simulations, the tuning width $C$ of the PCs’ receptive fields was set to match the noise in their internal estimate of location (the sensory noise) $R$. The place field centres were distributed uniformly throughout the environment according to a specified density. The agent explored the environment according to a random trajectory at a fixed velocity.

At the start of a trial, the initial location estimate distribution was set as a delta function centered at the current location. The high precision of this initial estimate was important for two reasons. Firstly, since the learning rate is proportional to the activity of the GCs above their RMS level, a highly peaked distribution meant that
learning occurred more quickly. Thus, the PCs active at the current location formed strong associations to the GC sheet and acted as an ‘anchor’ thereafter. Secondly, a highly precise initial estimate meant that the animal could travel further before that estimate generated.

To test the ability of the system to form stable grid patterns, the measurement noise, PI noise and PC density were systematically varied. In all simulations, initially no stable grid firing was present as the system was relying purely on path integration to track its position. At this initial stage, the contribution of the sensory input to the overall estimate was weak, since the distribution resulting from the unstable PC-GC weights was broad (untuned) (Fig. 4.7A). However, as the agent continued to explore the environment, the PC-GC weights became increasingly tuned until at
Fig. 4.6: Diagram of the integration process A The grid sheet firing rates are updated according to the path integration movement B Learning occurs between the place and grid cells based on the aposteriori (integrated) estimate of state C Place cells firing rates are multiplied by their rates to generate the sensory input D The PI and sensory estimates are combined on the GC sheet E Outputs from each of the sensory and measurement distributions are transformed by logarithmic firing rates F The log-posterior distribution is fed through an exponential activation function to complete the circuit G A Recurrent circuit normalises the overall firing rates of the posterior distribution.

A critical point, the overall estimate became accurate enough to produce grid-like firing (Fig. 4.7A, B).

By isolating different stages of the three stage update process it was possible to visualize the grid pattern that would be produced from either pure PI or sensory inputs independently. In all simulations, the integrated estimate produced grid patterns that were more stable that those based on either pure PI or pure sensory input (Fig. 4.7D). Moreover, a stable grid pattern emerged from the integrated estimate ahead of the pure sensory estimate, confirming that the principle of cue integration was able to localize to a higher accuracy than either of two independent cues.

In all trials where convergence was successful the PC-GC weights converged to qualitatively the same structure as weights that were learned under noise-free PI (Fig. 4.7C), although their tuning was broader due to the measurement noise. Convergence was sensitive to the noise parameters. When the measurement noise (or equivalently the PC tuning, since \( C = R \)) or PI noise was too high, the system failed to converge (Fig. 4.7E).

However, the same was also true for very low levels of noise. Although this might initially appear as a failure of the model, it in fact emphasizes the central problem of hard-resetting mechanisms. When the measurement noise is set to very low levels relative to the PI noise the system approximates a ‘hard-reset’ since the sensory input is considered much more reliable than the PI input. In some cases, this effect lead to a catastrophic failure mode whereby strong initial associations cause the grid pattern to become ‘stuck’ at the initial location. More generally, strong associations formed on first exposure to a possibly erroneous location were likely to ‘reset’ the animal upon revisiting, preventing the system from converging to the correct structure over time.

Conversely, when PI noise was too high the system suffered from a catastrophic collapse of the activity pattern. However, this failure mode is likely an implementational flaw resulting from the precision of the current location estimate exceeding the precision of the environmental discretization.
Fig. 4.7: A PC - GC weights stabilize over time, producing a stable hexagonal grid pattern. (Right) Despite the noise in each PC’s firing being uniform across the environment, weights near the boundaries and corners self-stabilize first by virtue of a reduced trajectory through these points. B Stable grid patterns develop in non-rectangular environments. (Bottom-right) The grid pattern can occasionally form local representations separated by dislocations. C Stabilization of weights: Each hexagonal tile represents the weight from a single PC to the GC sheet. Weights learned under perfect perfect PI (noise free; Left) are identical to those formed under noisy PI (Right). D Under certain conditions, a stable grid pattern may emerge in the integrated estimate, despite the PI noise being too great and the sensory associations too immature to generate a stable pattern from either input independently. E Gridness score following a fixed learning trial as a function of the movement uncertainty ($Q_0$), measurement uncertainty ($C_0$) and the PC density ($N/m^2$). Grid scale $\lambda = 0 : 2m$. The grid and PC weights only become stable within a narrow parameter regime. If the uncertainty in either the sensory or measurement input is too high, weights remain unstable (low gridness score) for the remainder of the trial. Reducing the uncertainty in the sensory input leads to larger grid scores, whereas reducing the uncertainty in the movement input eventually causes the grid representation to break down. Grids are only stable above a critical PC density. E Stable convergence is sensitive to the learning rate. The grid scale of the readout corresponds to the intrinsic grid scale parameter.
The system was also sensitive to the density of PC coverage, failing to converge beneath a critical density ($\sim N = 500m^{-2}$). Presumably, below this critical density the coverage was insufficient to generate a smooth and continuous input to the GC system. Another study (Dordek et al. (2015a)) found that when extracting principal components from Gaussian shaped PCs, the resulting grid patterns were proportional to the width of the place fields\footnote{In personal re-creations of this study, it was found that convergence of the PCs was also dependent on the place field coverage (density).}. The same requirement was true of the proposed system; it was found that the place field width needed to increase in proportion to the grid scale in order to guarantee convergence (figure not shown).

Lastly, the convergence was also strongly dependent on the learning rate. When the learning rate was too high, strong associations formed on first exposure to the environment caused the activity pattern to become ‘stuck’ at the starting location.

### 4.3.2 Attractor dynamics

Next, the system was analyzed to test whether the GCs across the simulated module displayed attractor-like dynamics, which are characterized by two main properties.
Firstly, the grid patterns from each module should share the same orientation and spatial scale. Secondly, the firing patterns of each GC should be spatially offset such that their combined firing rates tile the environment.

The spatial offset of each GC was calculated as the peak in the cross-correlogram between grid pattern $G_i(x)$ and a randomly chosen base grid pattern $G_0(x)$. The analysis confirmed that the spatial offsets were uniformly distributed through phase space (4.8B, C). Moreover, the peak correlation values were similar across the module, suggesting that each pattern was indeed a spatially offset copy of the others (Fig. 4.8B).

4.3.3 Response to environmental manipulations

Global rescaling: Barry et al. 2007

It has been experimentally observed that grid cells parametrically rescale in response to environmental rescaling. Barry et al. (2007) found that the grid scale under-responded when one of the walls of a familiar 100x100cm environment was compressed to 100x70cm, rescaling on average by 47.9\% (6 rats, Fig. 4.8D). The original grid scale was unaffected upon decompression to the original environment. Stensola et al. (2012) found that grid modules rescaled independently in response to the same environmental change. In a familiar 150x140cm compressed to 150x100cm, the authors report that rescaling tended to occur on an ‘all-or-nothing’ basis, with large grid scales tending to rescale completely whereas smaller scales typically showing no rescaling response. Moreover, Barry et al. found that on repeated compression/decompression trials, the magnitude of the rescaling decreased (Fig. 4.8D).

This rescaling behaviour clearly demonstrates that GCs are at least partly driven by sensory inputs, rather than relying purely on path integration. Geometrical changes are likely driven by BVCs, which are thought to project to PCs and indeed, previous modelling has shown that PC responses can be constructed from BVC responses (Hartley et al., 2000). Later experiment showed that changes in place fields in response to environmental manipulations could be explained using this BVC-PC model (Lever et al., 2002).

The model was first tested in its ability to reproduce the basic rescaling response observed in Figs. 4.8(C, D). To simulate the sensory changes arising from the environmental rescaling, the position and variance of the PCs were both scaled in proportion to the environmental rescaling. When the learning parameter was left unchanged from the value that facilitated learning of the stable pattern in the uncompressed environment, the grid firing pattern was rapidly destroyed upon compression. Following the compression, the measurement and sensory inputs were in discord, causing learning away from the previously stable weights and causing the grid pattern to be disrupted.
In contrast, when the learning rate was set to $\tau_w = 0$, grids rescaled perfectly, preserving their original firing pattern when the environment was de-compressed (Fig. 4.8C, Bottom).

Deformations caused by pre-learned associations

PCs are known to ‘remap’ in response to novel environments, some PCs shifting their place fields, changing their firing rates or becoming silent. The population firing of PCs in CA1 and CA3 thus represents a unique code and is thought to represent the distinction of those environments in the cognitive map. However, disambiguation by PCs is imperfect; PCs may remap in context to changes in environmental geometry (Muller and Kubie (1987b); Lever et al. (2002b)), colour, and odor (Anderson and Jeffery (2003)) and textures (Lee et al. (2004)), among others. Not all PCs respond identically however, some remapping whereas others remain unchanged.

‘Partial’ remapping (Bostock et al. (1991)) accounts of PCs suggest that subsets of PCs might encode certain features of an environment. However, full remapping in response to changes in a single ‘feature’ (e.g. wall colour) suggest that these features must be associated, such that a particular conjunction of features represents the code for a given environment.

Geometrical information is a strong determinant in PC firing (Hartley et al. (2000); Lever et al. (2002b)) and is thought to be mediated by BVC firing (Solstad et al. (2008); Lever et al. (2009a)). Thus, geometry might in principle be an indirect (or direct; Hardcastle et al. (2015)) determinant of GC firing (Evans et al. (2016)). A recent study showed that the rotation of one wall in a rectangular box produced displacements in the previously stable place and grid fields (Krupic et al. (2018)).

It has been observed that GCs in non-rectangular environments (Derdikman et al. (2009); Krupic et al. (2015)) show deviations from the uniform hexagonal grid pattern. In one such example, the grid pattern in a trapezoid appeared to locally align with different non-perpendicular edges (Fig. 4.9F, Right). In the same study, the animal had prior experience of a rectangular environment.

I hypothesized that given initial exposure to rectangular environments, the HPC-mEC might develop useful ‘features’ with which to code for these environments. When exposed to a novel environment, in absence of other experience it is possible that these features might be imposed in the form of ‘prior’ or ‘expected’ features. Stated another way, the animal might view a novel environment through a ‘prism of experience’. Specifically, it is proposed that these features represent the expected geometry of the environment, which might be represented by BVC firing and their associations with PCs.

To test this hypothesis, the BVC model of PC firing was used (Hartley et al. (2000)).
Initially, a uniform population of place fields was assumed in a rectangular environment. These abstract place fields were then recreated by a learning a set of BVC-PC weights to a population of BVCs, whose receptive fields are defined by the equation:

\[
b_i(r(\theta), \theta) \propto \frac{\exp[-(r(\theta) - d_i)^2/2\sigma_{rad}(d_i)]}{\sqrt{2\pi\sigma^2_{rad}(d_i)}} \times \frac{\exp[-(\theta - \psi_i)^2/2\sigma_{ang}]}{\sqrt{2\pi\sigma^2_{ang}}} \tag{4.34}
\]

where \(\sigma_{ang}\) is a constant describing the angular tuning, \(\sigma_{rad}(d_i) = (d_i/\beta + 1)\sigma_0\) the distance dependent radial tuning where \(\beta\) and \(\sigma_0\) are constants. \(r\) and \(\theta\) are the allocentric (world-related) distance and bearing to a boundary element relative to the agent’s location. \(d_i\) and \(\psi_i\) are the preferred distance and bearing of BVC \(i\). The overall firing of a BVC is obtained by integrating its responses to all boundary elements:

\[
B_i(x) = \int_0^{2\pi} g_i(r(\theta), \theta) d\theta \tag{4.35}
\]

All parameters were set to the values described in Barry and Burgess (2007). PC firing was then determined by a weighted sum of BVC inputs:

\[
P_i(x) = S(W_i B(x) - T_i) \tag{4.36}
\]

\[
S(u) = 1/(1 + \exp(-5u)) \tag{4.37}
\]

where \(S(u)\) is the logistic activation function and \(T_i\) is the firing threshold of PC \(i\). The weights and thresholds were fitted to maximize the correlation between the BVC-simulated and abstract (2D Gaussian) place fields in a rectangular 2D environment, however the weights can also be learned in more biologically plausible manners (Barry and Burgess (2007)).

The PC-GC connections were then learned in a rectangular environment by running the model as in previous simulations, producing a stable grid pattern (Fig. 4.9F, Left). The agent was then introduced to a novel trapezoidal enclosure.

Driven by the underlying BVC firing, PCs responded the environmental manipulation by shifting their fields (Fig. 4.9D), although some fields ceased to fire (red dots). Importantly, the movement in the PCs drove a similar response in the resulting grid pattern (4.9F, Right). In the wider end of the trapezoid, the grid pattern was largely unperturbed. However, grid fields in the narrow end increasingly aligned with one or two of the long edges.
Fig. 4.9: A Initially, grid patterns are identical in two perceptually similar compartments. When the animal is allowed to navigate between these two compartments the spatial phases of the local patterns shift so as to become globally consistent (Carpenter et al. (2015)). B Simulation in 1D. Initially, the grid patterns are mirrored, but as the agent is allowed to navigate between the two compartments PI forces the two to merge. C Example of predicted place field shifts generated by the BVC model (Hartley et al. (2000)) when the environment is morphed from a rectangle to a trapezoid. D All simulated place field shifts. Red dots indicate fields which either had multiple or no fields in the trapezoid. E Experimentally observed (Left: Krupic et al. (2015)) and simulated (Right) grid patterns following environmental morphing.
4.3.4 Global embedding of local representations

A major limitation of hard-resetting models is that once the sensory-GC associations are learned, errors or modifications to the map cannot be ‘unlearned’ since the sensory input will always override conflicting information from the PI system. As discussed, sensory information has associated with it uncertainty. In the context of the hippocampal formation, PCs are thought to be driven by multiple sensory modalities including vision, touch, audition and olfaction, all of which are susceptible to being mistakenly detected. Different environment can be constructed from the same materials but may be painted in different colours. Others might be identical in all respects other than their dimensions.

But what of the case of perceptually similar environments? Several studies have analyzed the response of PCs in this scenario (Skaggs and McNaughton (1998); Fuhs et al. (2005); Spiers et al. (2013); 4.9A), which are known to remap in response to contextual changes. These studies consistently found that at least in the short term, place fields were mirrored between the environments suggesting a strong drive from sensory cues. These effects can be easily accounted for by BVCs (Hartley et al. (2000); Grieves et al. (2018)), which fire in a specific allocentric bearing and distance to boundaries. On a population level, the firing rates of BVC across an environment thus provide unique signatures corresponding to specific environmental geometries.

GCs are also known to respond similarly, producing the same firing patterns in multiple corridors of the same linear track (Derdikman et al. (2009); 4.9A, Right) and initially in two perceptually identical environments (Carpenter et al. (2015); Fig. 4.9A). However, the latter study showed that when the animal was able to navigate between the two perceptually identical compartments along a narrow corridor, the GC firing patterns slowly converged over a timescale of 2 weeks such that they became globally consistent (4.9B). The result suggests that although GCs may be driven strongly by sensory inputs, PI eventually allows the system to disambiguate the two environments by travelling between them. However, disambiguation by PCs of two perceptually similar (but not identical) environments was demonstrated over similar time-scales (Lever et al. (2002b)).

GCs and PCs are known to respond to contextual changes (Fyhn et al. (2007)) on similar timescales. However, it is unclear whether the same is true in PI based disambiguation as the aforementioned studies either did not perform simultaneous GC and PC recording, or did not record over the same timescales as the Carpenter et al. (2015) study (Derdikman et al. (2009)).

To test whether principles of sensory integration could be used to disambiguate two similarly encoded local environments by simulating a simplified 1D version of the task presented in Carpenter et al. (2015). Initially, the agent was allowed to explore
two halves of a 1D linear track separated in the middle by a wall (4.9C). After an initial learning period (corridor closed), the wall was removed and the agent was allowed to traverse freely between the two previously separated halves of the track (corridor open).

Initially, it is assumed simply that PC responses are identical in both halves of the track, as would be the case if they were responding to environmental geometry or other sensory modalities. In the connected portion of the trial, a second population of PCs is introduced whose fields are local to one or other of the environments.

As expected, GC responses were mirrored in both halves of the track during the corridor closed phase. When the corridor was opened, sensory inputs continued to dominate over the disambiguating PI information, however over time the GCs eventually shifted their associations to the PCs whose fields were specific to either of the two halves of the track. In doing so, grid patterns between the two boxes slowly converged to form a globally consistent pattern (4.9C).
4.3.5 Saliency-based local deformation

Distortions from non-uniform PC densities

In all previous simulations, it was assumed that the place fields were distributed uniformly throughout the environment and shared identical tuning widths and firing rates. Experimental evidence suggests that this assumption may be an oversimplification. Place fields are more densely concentrated near entry ways (Spiers et al. (2013) and goal locations (Hollup et al. (2001)) and may be smaller nearer the edges of an environment (Hetherington and Shapiro (1997); Barry et al. (2006)).

Thus, the effect of biasing the place field properties across the environment was explored. Motivated by the findings of Stensola et al. (2015) who found that the grid patterns were often sheared about the corners of an environment, it was hypothesized that non-uniform place field properties, perhaps related to saliency or exposure, might produce distortions to the grid pattern.

This hypothesis was first examined in a simplified model which simply treats GC firing as a weighted function of PC drive (i.e. temporarily disregarding the PI component in 2). To learn the PC-GC weights, noise-free exploration was simulated over an initial learning period. The peak firing rates of the PCs were then scaled according to a ‘reweighting function’ $R(x)$, an exponential-polynomial function of distance from focal points $C = (c_1, c_2, ..., c_N)$:

$$R(\mu) = \sum_{c \in C} e^{-r_1(\mu_x - c_x)(\mu_y - c_y)}$$

where $\mu$ is the place field location and $r_1$ is a decay parameter. As $r_1$ increases, $R(\mu)$ becomes increasingly skewed towards the focal points. Note that due to the form of the observation model (a normalized weighted sum), re-weighting the PC firing rates is equivalent to modulating the local place field density.

Firstly, the analysis considered the effect of a re-weighting function with a single focal point in the bottom-left corner of a square environment (Fig. 4.10B, $C = ([0, 0])$). As the decay parameter was increased, the resulting grid pattern appeared to undergo an increasingly pronounced shearing pattern.

When the same re-weighting function was applied with two focal points in opposite corners (4.10C), the result was similar to another experimentally observed distortion (Stensola et al. (2015)).

The effect of the re-weighting was next explored by a simplified mathematical analysis (see chapter Appendix). Briefly, by assuming that the place and grid fields are composed of single and multiple Gaussian tuning curves respectively, with tuning
width $\sigma$, and that their initial weights are learned as a function of the correlation of their firing patterns, it is possible to prove that the resulting grid pattern is distorted according to:

$$\delta x = -\sigma^2 r_1(c_y - x)$$  \hspace{1cm} (4.39)
$$\delta y = -\sigma^2 r_1(c_x - y)$$  \hspace{1cm} (4.40)

I.e. a linear translation $\delta x$ in the $x$ direction is proportional to the distance of the coordinate from the focal point $c$ in the $y$ coordinate, and vice versa. This analytically obtained result is equivalent to a 2D shear transformation. The magnitude of the shearing also increased with the magnitude of the tuning width $\sigma$.

From the above result, the expected alignment offset was calculated by applying the shearing transformation in eq. 4.40 to an idealized hexagonal lattice consisting of three basis vectors $120^\circ$ apart (4.10E). From the sheared lattice points, the angles of each of the basis vectors can easily be calculated.

The analysis predicts that $A_{min}$ should increase as the decay parameter (or equivalently, place field corner concentration) increases (Fig. 4.10D, Left). A similar relationship is observed as a function of the PC width (Fig. 4.10D, Right). Although there is no explicit dependence of the orientation offset on the scale of the grid, the latter result would imply an indirect relationship due to the empirically observed scaling of field width with grid scale.

**Experience-dependent shearing and alignment offset**

The previous result was then tested in the full model (2). In these simulations, the distribution of place field centers was scaled according to the same re-weighting function as was used to scale the firing rates in the previous analysis (4.10A, Top-middle).

Again, the resulting grid pattern was sheared, resulting in an alignment offset of $7.5^\circ$. Interestingly, the shearing effect did not manifest instantaneously, but rather developed with increasing experience, mimicking experimental observations (Fig. 4.10 Bottom-middle; Stensola et al. (2015)). The resulting histogram of orientations across (100 trials) was also identical to experimental data (4.10A, Right column).

Thus, in the context of the full model (2), the experience-dependency can be attributed to a slow maturation of sensory connections. Initially, when the agent explores the environment the undeveloped PC-GC weights provide no input to the GCs, forcing the system to rely on exclusively on PI to generate the grid pattern.
However, as the weights mature, the sensory input to the system begin to dominate over PI, leading to an increased shearing effect (Fig. 4.10A, Middle-bottom).

4.4 Summary

4.4.1 A novel model of spatial localization

In this chapter, it was demonstrated that a GCs can under certain conditions solve a the SLAM problem on a modular basis, without interaction from the other GC modules. This is achieved without specific circuitry implementing SLAM specific algorithms (c.f. Cheung (2016)) that would be difficult to implement neurally.

A neural implementation was also presented based on simple, known dynamics. It is proposed that logarithmic firing rates and sharpening circuits may allow the system to perform probabilistic operations by summation (Pouget et al. (2013)). The shifter cell system (Zhang (1996); Burak and Fiete (2009)) was also generalized to the case where the distribution is broadened to incorporate movement noise.

Lastly, the model proposed is novel in the sense that no attractor dynamics are required to maintain a stable bump. However, the cells in the GC sheet maintain their spatial offsets over time and uniformly tile a given environment, reproducing to the observed properties of putative attractor network. Instead, the bump arises naturally from the integration of sensory and movement inputs. This is in part due to the sensory inputs being a weighted summation of PC inputs, which are themselves Gaussian. Furthermore, the model predicts that the activity pattern, in addition to its readout in real space, will degrade with lack of sensory inputs. This contrasts to the prediction made by CAN models, which assume that noise in the readout is due only to the bump and animal movement falling out of phase, and that the base attractor pattern should remain stable. This is an experimentally testable prediction, and further work will involve devising a suitable experiment.

4.4.2 Response to environmental manipulations

It was also demonstrated that probabilistic integration of sensory cues, rather than hard-resetting, allows the system to account for several experimentally characterized phenomena.

Firstly, the results show that the grid pattern responds parametrically to environmental rescaling (Barry et al. (2007); Stensola et al. (2012)) and interprets the phenomenon as dominance of sensory inputs over PI information. Whereas this account of GC rescaling is broadly in line with experimental observations, there is some suggestion that the rescaling response may be dependent on the GC scale whereby GCs with smaller scales tend to resist rescaling whereas GCs with larger scales remap completely (Stensola et al. (2012)). If this were the case, it might be
possible that rescaling only occurs when the sensory input is in conflict with the PI input. In the context of the proposed model, this would not occur if the rescaling magnitude were an integer factor of the grid scale, such that the boundary of the compressed environment aligned with another grid field. Importantly, it would also require that the dominant sensory inputs were at the borders of the environment.

Secondly, it was proposed that distortions to the grid pattern in non-rectangular environment might be the product of prior experience of different environments. By assuming PCs are generated by BVC firing, it is shown that the place fields will shift when a rectangular environment is morphed into a trapezoid. The resultant PC firing will drive GC responses according to this morphed shape, producing similar grid patterns to those observed experimentally.

Global embedding and GC driven PC remapping

It was also shown that GCs are able to unify previously local representations by virtue of PI. Simulations show a slow convergence of the grid pattern, mirroring experimental observations (Carpenter et al. (2015)). To my knowledge, no existing model is able to provide a satisfactory account of this phenomenon, although one study (Stachenfeld et al. (2017)) proposed an explanation whereby GCs represent an low dimensional encoding of the transition structure of the environment. However, their hypothesis is somewhat unsatisfactory in that to initially mirror the grid pattern requires similar trajectories in both environments. Secondly, the example of the 'global' fit provided in the paper does not appear convincing, instead suggesting that significant 'local' effects remain.

Saliency-based distortions

Lastly, it was demonstrated that by biasing the distribution of PC firing rates or field density, the GC is susceptible to experimentally characterized distortions (Fig. 4.10; Stensola et al. (2015)), which may be described by a shearing process about one or two location. The model proposes that experience-dependent distortions may arise from the competing nature of PI an sensory inputs, the latter becoming stronger over time as the PC-GC associations are matured. In addition to simulated results, a mathematical analysis of this phenomenon is provided, although it is emphasized that the results should not be interpreted too exactly, but rather considered as useful intuition. In reality, the exact distortions would be highly dependent on the shapes of the tuning fields and the nature of the re-weighting function, among other factors.

More intuitively, the results can be understood as a bias in location decoding towards overrepresented regions such that the GCs active at the biased location will be active over an inflated range. In the proposed system, the distortive effects are a 'bug rather than a feature', it is possible that such a representation might have behavioural advantages. For example, over-representing a hazardous area would
result in the perception of being closer than one actually was to the area, making greater allowances for error in location estimation than might otherwise result in potential injury. Recent evidence suggests that distortions to the metric map may also affect behaviour (Bellmund et al. (2018)).

Conclusions

The problem of integrating sensory inputs within the GC system has important implications for coding, since each module is proposed to perform this integration independently, meaning that an efficient decoding mechanism ([Fiete et al.] (2008a); [Towse et al.] (2014); [Mathis et al.] (2012); [Mathis et al.] (2015)) would have to function with this allowance built in. One study ([Mathis et al.] (2015)) investigated the decoding of elliptical GC patterns and showed little effect on performance and indeed, a simple mechanism based on maximum likelihood decoding would perform equally regardless of the distribution. However, this finding, if true might have implications for studies exploring the role of the optimal scale ratio between modules.

Finally, although the proposed system is able to operate under certain conditions, it is unlikely to reliably converge when noise is high or when the structure of the environment is more complex. Thus, the focus of this chapter was on the mechanism of probabilistic integration rather than map construction explicitly. However, the next chapter proposes an extension to the framework that will treat the SLAM problem more explicitly.
5. SLAM: HIPPOCAMPAL REPLAY AS OFFLINE INFERENCE

In the previous chapter it was discussed how cue integration in the hippocampal formation could help to explain several experimentally observed phenomena. Moreover, it was shown that the addition of Hebbian learning allowed the animal to correctly learn a cognitive map of its environment while exploring it for the first time. However, the results show that the convergence properties of the system are brittle, failing to converge under higher PI and sensory noise or when navigating more complex environments. This chapter begins by analyzing the SLAM problem in more detail and concludes by describing an augmentation to the model, allowing it to perform offline inference.

5.1 Simultaneous localization and mapping: A primer

5.1.1 Problem description

The simultaneous localization and mapping (SLAM) problem describes the difficult task of learning a map of an unknown environment, while at the same time using it to navigate under noisy conditions. The traditional definition of SLAM incorporates the idea of using both PI and sensory information in order to construct a consistent map. Although complementary, these two sources of information describe two different ways of navigating. PI is a relative estimate of position in the sense that it must always be referenced to an absolute location of space. The strength of PI information is that it inherently captures the metric structure of observations in space; if landmark A is observed ten steps before landmark B, the two must be ten steps apart. Conversely, sensory observations are non-relative but if correctly stored can immediately point to absolute locations in space.

However, there are good grounds for considering whether SLAM is even necessary for navigation, if a system could rely on either perfect PI or visual recognition. The state of the art in visual-inertial odometry, which uses both odometric (step-counting) and visual flow information to estimate PI, can be extremely robust to drift (< 0.5% of the trajectory length; Forster et al. [2017]). Such an approach would provide an exact metric description an environment and allow an agent to reason on the basis of that structure. Conversely, an ‘oracle’ place recognition system could in principle store the relationships between all observed landmarks and re-construct the topology of the environment from their mutual relationships.
Answering the question of whether SLAM is essential therefore requires the understanding that SLAM is not a single universal solution to a one-size-fits-all navigation and mapping problem. Rather, it is more a methodology describing how to approach these problems. The simple answer is therefore that “it depends”.

In practical terms, navigating based on PI is subject to the complexities and noise conditions of the environment. Even state of the art approaches would fail when navigating in the most challenging environments such as underwater, low light conditions or over uncertain and featureless terrain. More generally, even navigating with an acceptable degree of precision within more modest environments requires accurate sensors (high quality laser sensors or vision). This emphasizes a crucial aspect of the SLAM problem, which is the trade-off between performance and hardware cost. Rats are known to possess poor vision, whereas vestibular and odometric inputs by themselves are subject to drift \cite{Kelly2013}; Chapter 6, it is reasonable to thus conclude that rats would find it difficult to navigate purely based on PI.

The second intuitively simple problem that is nonetheless extremely difficult in reality, is that of visual recognition. As humans, we take for granted the ability to distinguish places and objects from one another. While humans and animals may well be adept at this task, owing in part to sophisticated understanding of geometries and textures, this ability is also strongly underlined by its conditioning on location \cite{Saleem2017}. One might consider the challenge of navigating by place recognition only in a forested environment or dense urban environment such as London’s Soho district, where the architecture is relatively homogeneous and the field of view is limited by the surrounding buildings. Added to this difficulty is the fact that places or objects are rarely observed from all angles, such that recognizing a familiar landmark might still be difficult if approaching along a novel trajectory.

The advantage of utilizing metric information is that places or objects that appear visually similar can be distinguished by their relative locations in space. Thus, a full SLAM approach makes the theoretically possible, but practically very difficult problem of place recognition manageable. Incorporating metric information is also extremely important in dynamic environments where objects cues might change their location.

In principle, localization based on topological representations of an environment are sufficient for navigation. One could imagine trying to move from $A \rightarrow B \rightarrow C$ by following a gradient (“when I move in this direction, my visual input looks more like $A$!”). An understanding of the transitions between landmarks can be compared

\footnote{At the time of writing, there are at least 237 coffee shops in London belonging to the chain ‘Pret a Manger’. I have previously made the mistake of assuming that I knew my location having caught sight of a ‘Pret’, only to find that it was in fact a different but identical site just around the corner. That is has happened several times implies that the rate of PaM’s expansion exceeds the rate at which I can revise my prior beliefs about their spatial density!}
to what is known in RL parlance as ‘model-free’ control. In model-free control, an agent seeks a goal by greedily optimizing its value function, where each state in an environment is assigned a ‘value’ with respect to the possibility of later transitioning to the goal location. However, most animals are known to be able to reason with their model of the world, allowing them to take shortcuts along previously unexplored trajectories. The possible utility of a ‘cognitive map’ for the purposes of RL was discussed in the introductory chapter of this thesis.

Constructing a topological understanding of one’s environment can be reduced to the problem of finding ‘loop closures’ ([Cadena et al. (2016)]). In a loop closure event, independent observations are identified as corresponding to the same location. Without these events, an agent navigating around a loop would interpret its environment as an “infinite corridor” (Fig. 5.1A). Loop closure is generally made easier by metric representations since two observations made nearby can help to infer that the observations are likely to be of the same landmark (even if from a different viewpoint). Loop closures using topological representations can be more difficult for the same reason.

The question of whether SLAM is “solved” is also inherently tied to the practical
problem at hand. For a robot equipped with comparatively rudimentary odometry sensors and an entry level laser scanner, mapping an indoor 2D environment can be considered practically achieved with an industrially acceptable failure rate (Robotics (2016)). However, state-of-the-art systems still struggle when environments are sufficiently complex or high speed requirements are imposed. Nonetheless, SLAM can be considered a comparatively mature field and modern research is broadly focussed on one of two areas. The first is in improving the robustness of existing solutions and standardizing approaches for improved industrial uptake\(^2\). The second is focussed on moving SLAM into the ‘perceptual age’ (Cadena et al. (2016)) with systems developing a higher-level semantic or physical understanding of their environment. Much like cognitive science and artificial intelligence (AI) research, SLAM has long been considered a distinct domain to machine learning (ML). Both AI and SLAM subsume aspects of ML and statistics to the extent that they are useful for solving the engineering requirements (in a computer science sense) of their respective domains. However SLAM, like much of modern AI emphasizes the need for a systems level approach.

It is therefore not surprising that, as has been the case historically in other areas of scientific research, the trajectories of the two fields are beginning to converge. In both domains there is a need for a less hand-driven approach to systems design. Interestingly, the role of ‘active-learning’ or self-guided exploration is being explored in a SLAM context. More generally, this can be understood from the perspective of goal-driven perception, which is to say that localization and mapping could be argued to be only useful within the context of the current task (Mirowski et al. (2018)). The cognitive perspective from the hippocampal field is similarly converging on the idea that some representations (spatial or otherwise) are formed with respect to task demands, as opposed to apriori in expectation of some unknown functions (Stachenfeld et al. (2017)).

**Formal description of the SLAM problem**

SLAM almost invariably refers to the either the ‘full SLAM’ or ‘online SLAM’ problems. The full SLAM solution requires that the trajectory of the agent state and map states be estimated after each new observation. Conversely, online SLAM only requires that the most recent state trajectory and map states be updated. Both can be expressed as computing the posterior density:

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\(^2\) At the time of writing this thesis, there is a distinct feeling that the age of driverless vehicles is upon us, although several people independently predicted that Jetpacks would be the primary mode of transport beyond the year 2000.
where $x_k$ is the current state vector describing the position of the agent, $m$ is a vector of inferred landmark locations, $z_{0:k}$ the history of observations, $u_{0:k}$ the previous movements and $x_0$ the starting location. The exact solution to the full SLAM problem is in general computationally intractable for states with arbitrary probability distributions, since the joint trajectory–map posterior state space quickly becomes too large as the robot progresses and increases the number of landmarks in the map. Both can be conveniently visualized as a factor graph (Fig. 5.1C). In factor graphs, nodes can either be described as variable nodes or factor nodes. Variable nodes represent either unknown variables to be inferred (e.g. the $k$-th location in the trajectory) or observations (e.g. the starting position $x_0$). Factor nodes are probabilistic constraints that describe the relationships between nodes on the graph.

Factor nodes can be largely summarized as either observation constraints or odometry constraints. Observation constraints describe the probability of making observation $z_k$ given that the location of the animal is known relative to a known map. Constraints of this type also require that the observation model is known. The observation model was discussed in the previous chapter, but it is re-stated here in its probabilistic form for clarity, making explicit its dependence on the current map:

$$p(z_k | x_k, m)$$  \hspace{1cm} (5.3)

Similarly, odometry constraints are described by the transition function between successive states:

$$p(x_k | x_{k-1}, u_k)$$  \hspace{1cm} (5.4)

A solution to the online problem then follows a two-step movement-measurement update process to recursively compute the posterior as new movements and observations are made.

One of the most important insights for the convergence of SLAM was the realization that errors in landmark observations are highly correlated (Durrant-Whyte and Bailey (2006)), with correlation decreasing with the pairwise distances between landmarks. Thus, even though a pair of nearby landmarks might be recorded with high error in absolute map space, the error in their relative distance measurements
monotonically decreases with more observations. The convergence can be understood visually by considering the factor graph defined earlier as an ‘elastic mesh’ (Fig. 5.1B), where the factor nodes are considered as elastic constraints between variables. When an observation is made, the resulting movement of its associated landmark node causes similar relative movement of its connected neighbours. Thus, information about one landmark can be propagated through the graph.

**Representation**

Formalizing a theoretical solution to the SLAM problem is of course only useful if a system exists for computing that solution. Since the joint location–map state space is almost always high-dimensional, a solution must then rest on choosing a suitable representation for that distribution that makes this computation tractable on a practically useful time-scale.

Broadly, these two approaches can be separated into landmark-based and occupancy-grid maps. In the former, an environment is treated as a sparse set of landmarks whereas the latter discretizes the state space and assigns probabilities of the existence of a landmark to each of the bins. The advantage of the latter is that the form of the distribution describing the estimated landmark’s location can be arbitrary, whereas the cost of computing and maintaining maps with a sufficiently precise resolution scales with the size of the environment, often becoming computationally intractable.

In contrast, landmark-based approaches are extremely data efficient and computationally attractive methods for representing the map distribution, but do not explicitly help with the data association problem. Association of sensory input with its corresponding landmark must be performed without the help of metric information. Moreover, the problem of separating space into salient ‘landmarks’ is non-trivial and can add substantial complexity.

Of course, the notion of maintaining a map of landmarks makes the implicit assumption that landmarks are point-objects. In some cases this simplification might be justifiable such as the when places may well be denoted as having a ‘centre’. However, when the detailed structure becomes relevant to navigation, as would be the case in a forest or urban scene when the agent would ideally need to avoid bumping into objects, a structural understanding of objects becomes more important.

In the case of landmark-based representations, landmarks might refer to features such as lines and corners (Mur-Artal et al. (2015)) or more complex geometrical descriptors (Lu and Song (2015)), where the relationships between features of the same landmark may also be encoded probabilistically.

Lastly, the question of representation also extends to the observation and movement
models. As is the case of the map’s representation, both must be encoded in a form that makes computational optimization as efficient as possible while still respecting their statistical structure. Both are highly dependent on the environment and hardware available, however in many cases realistic assumptions can be made that consider the problem greatly.

5.1.2 SLAM and the hippocampus

Attractor based SLAM

The first work to bridge the gap between spatial navigation research in neuroscience and robotics was the RatSLAM project (Milford et al. (2004)). RatSLAM was originally developed as a biologically plausible system for performing SLAM in advance of the discovery of GCs. The original model bears similarities to the present model, using a 3D network of ‘pose cells’ to represent the current location and heading direction of the animal modelled on rodent PCs and HDCs. However, the system implements attractor dynamics in the pose cell network such that multiple hypotheses about location compete and eventually merge together (so as to represent a single estimate), unless sustained by constant stimulation from a population of ‘view cells’. The attractor network was implemented with square periodic connectivity such that a bump of activity would ‘flow’ off one edge to and the wrap to the opposite one. However, the attractor dynamics prevent the system from maintaining a true probabilistic representation of location over time. Moreover, the mechanism of integration does not account for the relative certainty of the visual and current position estimates, instead being based on a simpler thresholded stimulation mechanism.

Following the discovery of GCs (Hafting et al. (2005)), the RatSLAM system was updated by wrapping the attractor dynamics on a hexagonal sheet, producing grid like responses when mapped against the location of the agent in space (Milford et al. (2010)). Notably, since the 2D network tracked the distribution of heading direction as well as location, typical grid-like pose cell responses were also conjunctive (Sargolini (2006)).

The RatSLAM project was notable in that most simulations were performed in embodied robots which mapped real environments. Accordingly, although the models were designed for biological realism, their success as a whole was evaluated on their performance as SLAM systems, as opposed to a detailed comparison of the readout of the pose cells against physiologically characterized cell types. Lastly, the models did not speculate on the putative interaction between place and grid cells, instead relying on either one or other cell type (Milford et al. (2004) and Milford et al. (2010) respectively) at any one time.
Particle Filters and FastSLAM

Unlike RatSLAM which was largely based on recursive filtering approaches to the SLAM problem, Cheung (Cheung (2016)) based his system on the particle filter, a probabilistic approach which treats the problem of dealing with the large state-space of possible poses and maps by utilizing sequential importance sampling (SIS). The particle filter forms the basis of the popular ‘FastSLAM’ system (Montemerlo et al. (2002)), a landmark advance in SLAM research and the state-of-art in the field until relatively recently.

Without delving into the mathematical detail an initial population of ‘particles’ are sampled from the initial pose of the animal and initialized with hypotheses about the map. A larger population of particles is able to represent the true distribution in greater detail. As the agent navigates, each particle is updated independently according to the movement function and receives observations from sensory inputs. As this process continues, each particle builds an independent hypothesis of the current state of the animal and map structure.

The crucial aspect of the particle filter’s operation is the resampling step. After each observation, the observations are compared against a prediction generated by each particle, given its own hypothesis about state and trajectory. The particles are then resampled with a weight that reflects the match of the predicted to actual observations. Thus, particles whose world hypotheses match to the current world input are more likely to be preserved while those with conflicting hypotheses are likely to be culled.

Unlike Milford et als. approach, Cheung was able to show that his system reproduced several important characteristic features of empirically observed GCs, including deformation in linear environments and rescaling to environmental inputs. However, as discussed in the previous chapter it is unclear whether particle filtering is a biologically plausible approach, nor does it naturally explain the uniform distribution of GC spatial phases observed experimentally.

5.1.3 The anatomy of a modern SLAM system

The work discussed above made great strides to establishing tangible links between viable SLAM systems and the broad dynamics of the hippocampal formation. Clearly, SLAM research represents a rich and complex framework for studying the complex phenomenology of experimentally characterized spatially related cells. However, there are several outstanding features of GCs and GCs that current models have yet to reproduce.

It was demonstrated in the previous chapter how a comparatively simple system might explain experience-dependent distortions to the grid pattern (Krupic et al.
In the online system presented in the previous chapter the GC firing rates encoded the current location distribution whereas the joint location-map distributions were encoded in the PC-GC weights. In this chapter, the ‘online’ system is augmented to store the joint map-map relationships as Gaussian functions in the recurrent PC-PC weights.

Earlier, the importance of correlations between landmarks for successful convergence was discussed. In the elastic mesh analogy, the convergence process corresponds to a gradual ‘stiffening’ of the pose graph. However, the online system presented so far does not explicitly account for these correlations during learning.

The anatomical mapping to the relevant joint distributions \( p(\cdot, \cdot) \) is illustrated in Fig. 5.2. In the online system, the firing rates of the GC population represent the current distribution over location \( p(x) \). Similarly, the joint landmark - location distributions \( p(x, m_i) \) are encoded in the PC-GC weights. However, the joint distributions between the landmarks are not explicitly encoded.

In this context, the recurrent GC weights could be interpreted as the joint probability distribution between discrete states, conditional on the current movement vector. In these simulations, this feature is assumed to be prelearned and hardwired, however several studies have explored the possibility of learning this transition structure based on the animal’s trajectory (Widloski and Fiete (2014b); Stachenfeld et al. (2014); Dordek et al. (2015a)). The notion that the transition structure could be learned based on the trajectory of the agent is an interesting and appealing future direction of research.
In contrast, the recurrent weights in the PC population in the proposed model are not utilized. However, unlike the explicit discretized representations encoding the existing agent and landmark distributions, a joint distribution based on unitary PC-PC connections might at first seem to be limited in its ability to sufficiently capture their statistical relationship (i.e. the probability of observing one landmark given an observation of another). However, state and landmark locations are much more uncertain and potentially multi-modal and are typically not described well by a compressed set of parameters, such as the mean and variance of a Gaussian.

In contrast, the statistical relationship between landmark could be argued to be much better described by a simpler form. Relative landmark locations are subject to lower variance than estimates of absolute state or landmark location, since the error in the absolute location is itself correlated (the basis of the convergence property of SLAM). Secondly, there is an established practice in the robotics community of linearizing measurement models to great effect. Much of these assumptions are based on the sensing hardware available which must physically compute a range estimate. In many of these systems, a common assumption is that the noise in the estimate increases in proportion to the distance.

In the case of observing the pairwise distance between a pair of landmarks (PCs), since in the proposed system their relative angular bearings are not considered their relative pairwise distance could be captured elegantly by a Gaussian distribution with mean equal to the estimated distance and variance equal to that same distance scaled by a noise parameter. The scaling of noise with distance is an assumption that was also made in the PI system, where the variance in the movement estimate is proportional to the agent’s velocity. Importantly, this would allow both the mean and variance to be captured by a single parameter, if the noise scaling factor were known to the system. It is thus proposed that the recurrent PC-PC connections present a natural medium for encoding this information. By doing so, all the relevant joint probabilities are encoded with an precision that is matched to their statistical structure (Fig. 5.2).

**Graph-based SLAM**

Whereas the graphical representation illustrated in Fig. 5.1C is a useful way to visualize the structure of the SLAM problem, it can also be used as a basis for its solution. Initial approaches ([Lu and Milios (1997); Thrun and Montemerlo (2006)]) were posed as solutions to the full SLAM problem, where the factor nodes graph contained nodes representing all observation and transitions, in addition to the variable nodes encoding the corresponding unknown pose and landmark states. A solution to the SLAM problem is then defined entirely by the minimization of an appropriate cost function (typically maximizing the likelihood of all observations by forming hypotheses over a likely map and trajectory).
Graph-based approaches abstract the problem from the SLAM domain, essentially posing it instead as an optimization problem and allowing the techniques to profit directly from advancements in sparse linear algebra and graph-based optimization (Grisetti et al. (2010a)). For this reason, graph-based methods are typically known as ‘back-end’ approaches and are coupled with ‘front-end’ approaches which deal with constructing the graph and performing navigation.

Modern graph-based approaches represent the current state-of-the-art approach to performing SLAM, having largely superseded particle filtering approaches. Their relative speed is due in large part to advancements in the speed of optimization techniques and improved understanding of the structure of the SLAM problem. However, this optimization process is still vulnerable to settling in local minima (5.1.D) and costly when the state space grows, leading to several ‘hybrid’ solutions such as the ATLAS framework (Bosse et al. (2003)) which uses a Kalman filtering approach to construct local maps, then fuses these local maps with back-end graph-based optimization, a process known as hierarchical SLAM (Estrada et al. (2005)). The possible advantages of using a GC like representation of space has not been explored, however the concluding section of this chapter will discuss this point in more detail.

5.1.4 Overview of chapter

So far, the discussion has presented an overview of the structure of the SLAM problem and described current solutions. Previous work bridging these concepts to the hippocampal formation and outstanding questions were also outlined.

Secondly, the system developed in the previous chapter was analyzed in the context of existing models. The existing system can be described as a limited solution to the SLAM problem based on occupancy-based mapping. Importantly, in all simulations, the data association problem is not considered, which is the task of identifying landmarks as unique from one another, although in principle this could be mediated by reciprocal connections from GCs to PCs.

The previous discussion concluded that a well-designed SLAM system would need to store and utilize the correlations between landmarks that are in most cases crucial to convergence. It was proposed that these correlations could be encoded in the the recurrent weights of the PC population, where the synaptic strength might elegantly encode the mean and variance of a Gaussian distribution, assuming a known scaling factor.

This chapter therefore describes an augmentation to the current system that both encodes and utilizes the information stored in the recurrent PC-PC connections. The mechanism is based on graph-based approaches, which treat SLAM as an optimization problem. Crucially, the analysis draws parallels between this solution
process and the phenomenon of hippocampal replay (Foster and Wilson (2006a)),
on which is provided a brief introductory review. Thus, the proposal is that replay
might represent an optimization over the structure of hippocampally encoded space,
making several experimentally testable predictions.

5.2 Algorithms for probabilistic inference

5.2.1 Spring mesh network and MDS

As introduced earlier in this chapter, relative measurements of pairs of landmarks
can be understood by analogy to the elastic mesh in Fig. 5.1B; Durrant-Whyte and
Bailey (2006), whereby nearby landmarks are connected by a spring with a preferred
length (the true pairwise distance) and an elastic constant (rigidity) that is some
function of the inverse of the distance. The rigidity-distance relationship in the
proposed system would reflect the increasing uncertainty of distance measurements.

If the pairwise measurements are exact, there is a single valid solution for the relative
locations of the landmarks. Indeed, given random starting locations such a mesh
would relax to this configuration as the solution that minimised the total elastic
energy in the system:

\[ S = \sum_{1 \leq i \leq n} \sum_{1 \leq j \leq n} w_{ij} (\delta_{ij} - d_{ij}(X))^2 \]  

where \( \delta_{ij} \) and \( d_{ij} \) are the estimated and true pairwise distances respectively and \( w_{ij} \)
is the rigidity of a connection. \( X \) represents the absolute estimated locations of the
landmarks.

In the formulation in (5.5), the notion of distance can be generalized beyond the Eu-
clidean sense, describing exactly the multi dimensional scaling (MDS) algorithm.
MDS is most commonly used as a data visualization technique, where the cost func-
tion is minimized to find a parsimonious projection of a potentially higher dimensional
set of nodes (landmarks) to a lower dimensional manifold that preserves some notion
of distance in the higher dimensional space.

However, in the SLAM problem there is additional information present, i.e. the
prior beliefs over the locations of each of the nodes in space. The cost function in
this case can be augmented:

\[ S = \sum_{1 \leq i \leq n} \sum_{1 \leq j \leq n} w_{ij} (\delta_{ij} - d_{ij}(X))^2 + \sum_{1 \leq i \leq n} r_i ||x_i - x_{i0}||^2 \]  

where \( x_i \) and \( x_{i0} \) are the current and prior beliefs over the location of node \( i \) and
\( r_i \) represents the confidence in it its prior belief. Continuing with the spring mesh
Fig. 5.3: Illustration of the Belief Propagation algorithm. A message from a given PC to its neighbour describes the broadcasting PCs belief about its neighbours location, conditioned on the broadcaster’s own self-estimate. Since only the pairwise distance between PCs is encoded in the recurrent weights, these messages take the form of rings of a corresponding radius. Here, B and C each send messages expressing their beliefs about A’s location. Over successive message cycles, A refines this belief. Note that A will also be broadcasting messages back to its own neighbours. M denotes the number of messages.

analogy, minimizing the cost function in 5.6 corresponds to finding the energetic minimum of a mesh whose nodes which are also connected to absolute locations in space (an elastically anchored mesh).

How does this seemingly physical problem correspond to the inherently probabilistic task of finding the maximally likely solution to the SLAM problem? The insight comes from re-casting the minimization of the above cost function in Bayesian form. If it is assumed that the likelihood of pairwise distances reduces with a Gaussian shape away from the observed pairwise distances and assume a Gaussian distribution over the prior locations, the posterior probability of a given node configuration can be written as:

\[
P(X) = \prod_{1 \leq i \leq n} \prod_{1 \leq j \leq n} \exp(-w_{ij}(\delta_{ij} - d_{ij}(X))^2) \prod_{1 \leq i \leq n} \exp(-r_i(x_i - x_{i0})^2) \]  

(5.7)

i.e. the product of the pairwise factors with the prior beliefs. Thus, maximizing 5.7 is equivalent to minimizing the negative log likelihood, which reduces again to eq. 5.6. Thus, the energetic solution to the anchored spring mesh is exactly equivalent to maximizing the posterior likelihood of the node positions, given some pairwise and absolute distance estimates.

5.2.2 Belief propagation and message passing

The anchored spring mesh analogy could map to the hippocampal system considered up to this point, with the additional complexity that the prior beliefs over the
locations of the PCs is encoded fully in the weights to the grid cells, rather than being simply described by a set of Gaussians with mean and variance.

States another way, the Gaussian prior in eq. 5.7 must be replaced by a fully represented distribution, which is encoded in the PC-GC weights (5.2). The Gaussian relationships between landmarks could be encoded in the PC-PC weights, for example in the densely recurrent network of CA3.

Typically, the formulation in 5.7 could be solved using efficient numerical techniques such as the Gauss-Newton or Levenberg-Marquardt algorithms. Both are simple to implement and are based on gradient descent from a suitable initial starting estimate. However, since the system must maintain a probabilistic estimate of the joint distribution, such methods are unsuitable since such the problem is not one of maximization or minimization to a point estimate. The key question is instead how to maximize the equivalent to 5.7 when the prior beliefs cannot be described by Gaussian functions.

Since no closed form exists and the problem is highly non-convex (Naseri and Koivunen (2017)), it is instructive to turn to approximate inference methods. There are three principal methods for performing approximate Bayesian inference. Variational methods find an analytical solution to an approximate form of the prior distribution, where the form of the approximation is chosen from a family of simpler and analytically tractable functions. Markov-Chain Monte Carlo techniques approximate a solution to the posterior by directed sampling.

A third technique, belief propagation (BP; Pearl (1982)) is an instance of a broader class of message-passing algorithms for performing inference on graphical models that take advantage of their intrinsic structure to simplify the inference problem. Although developed for directed acyclic graphs, ‘loopy’ BP (Murphy et al. (1999)) on undirected graphs has been shown to work well in practice.

BP can be defined as an iterative, local message passing algorithm, where a broadcasting node computes its ‘belief’ about its associated variables (the receiving nodes), communicates these beliefs and receives messages from its neighbours, then updates its belief and repeats (Fig. 5.3).

BP has two especially attractive properties as a candidate method for solving the optimization problem in a neurally plausible fashion. Firstly, BP is inherently distributed in its nature. Each node makes computations based on its own observations and does not require information about nodes in the graph other than those to which it is connected. Secondly, the computations performed by each node are relatively simple.

3 “Divide and concur”; Yedidia (2011)
These properties have made BP a popular choice in inherently distributed domains, where low computation and communications requirements are desirable as in the case of wireless sensor networks, which must collectively reach agreement given uncertainty about their relative positions (Wang et al. (2010); Ihler et al. (2005)).

These same features are of course shared by network of neurons. Broadly speaking, message-passing in the neural context could be interpreted not as a specific algorithm, but as a general principle describing the signalling of information between neurons so as to optimize some network function. These principles have been studied most often in the context of predictive coding (Rao and Ballard (1999); Lee and Mumford (2003); Friston (2005)). The predictive coding hypothesis broadly states that the brain is actively engaged in predicting sensory input so as to avoid ‘prediction errors’, in contrast to the view that sensory processing occurs in a predominantly feedforward fashion. Much of the early work was based around cortical processing hierarchies such as those involved in vision (Rao and Ballard (1999); lee2003hierarchical). As stated by Mumford (Mumford (1992)),

“In the ultimate stable state, the deep pyramids would send a signal that perfectly predicts what each lower area is sensing, up to expected levels of noise, and the superficial pyramids wouldnt fire at all”.

Thus, in the equilibrium state, messages from neuron to neuron no longer carry ‘surprising’ information, instead only reiterating what to each neuron what is already ‘known’.

5.3 Hippocampal replay: a brief primer

Hippocampal neurons have been known to increase their firing rates during sleep since the observation of short periods of high-frequency oscillations in the local field potential (LFP), superimposed on a lower frequency modulatory component (O’Keefe and Conway (1978)). These ‘sharp-wave ripples’ were later found to be associated with highly correlated reactivations of place cells whose firing fields overlapped in waking exploration of the animal’s environment (Wilson and McNaughton (1994)). Remarkably, later studies found that not only did these reactivations reflect co-activity, but they could also recapitulate the precise relative timing of the firing, such as to reflect sequences of activity experienced during wakefulness (Skaggs and McNaughton (1996); Lee and Wilson (2002); Foster and Wilson (2006a); Diba and Buzski (2007)). However, these sequences were compressed in time, typically representing the experienced trajectories at an 20× accelerated speed (Pfeiffer and Foster (2015)).

‘Replay’ events were later found to also occur during awake but ‘offline’ behaviour such as grooming, eating or pausing at decision points during navigation (Foster and
Replays are typically directional, beginning from the animal’s location and proceeding either forwards (Diba and Buzsíki (2007)) or backwards (Foster and Wilson (2006a)) along previously experienced trajectories. The directionality may reflect differing functionality; reverse replays are most often associated with pauses after reaching a goal location and forward replays occurring more often preceding movement initiation (Diba and Buzsíki (2007)), suggesting distinct roles in consolidation and planning, respectively. However, replay trajectories can also be initiated in locations other than the current animal’s location (Davidson et al. (2009a)) even during awake exploration. Lastly, replay trajectories have been demonstrated to piece together previously independently experienced trajectories (Gupta et al. (2010)).

Despite clear evidence for replay in the hippocampus, comparatively little is known about similar reactivations in mEC. Interestingly GC replay has been observed to occur both in parallel with (´Olafsdóttir et al. (2016)) and independently of (ONEill et al. (2017)) replay in HPC, a recent finding even suggesting that GCs may be necessary for hippocampal replay (Yamamoto and Tonegawa (2017)). However, the original report of coordinated HPC-mEC replay found that replay events preceded mEC events by 10ms. Theoretical understanding of the HPC-mEC interaction during replay is therefore not well understood overall; no model currently exists to describe the role of both.

Several models exist which to describe replay events in PCs. The first models assumed that replay could be generated simply by virtue of the direct associations between PCs with nearby place fields driving each other in sequence. The first shortcoming of these models is that they cannot account for remote replay events (Davidson et al. (2009b)). The second is that they predict that associations should be strengthened as a result of replay and should therefore become faster over time (Foster (2017)), contrasting with the finding that replay sequences tend to slow down on later laps of the same linear track (Foster and Wilson (2006a)).

The second important class of models relates replay to the theory of RL. The function of reverse replay in this context is fairly straightforward; reverse reactivations from a goal location may serve to retroactively attach places (and trajectories) with values (Foster and Wilson (2006a)). However, reconciling forward sweeps with RL is more problematic. In a Markov decision process (MDP), running backward sweep from a goal location is an efficient solution for determining the optimal trajectory through a sequence of states with associated decisions (actions). Given the known value of the goal location, one could take one iteration backwards and considering all possible states at that time, assign the action to those states that is most likely to lead to the goal location. This method can be propagated as far back in time as is necessary, building optimal trajectories for each possible starting state. In contrast, forward
sweeps are an *inefficient* method for performing planning - moving forwards through
a state space to reach the optimal goal requires evaluating all possible combinations
of trajectories.

A recent model proposed a novel framework for explaining replay in the context of
RL ([Mattar and Daw (2017)]). The authors proposed that states in the MDP (PCs)
are re-sampled in order to improve the behavioural policy of the animal (the actions
taken from a given state). The utility of sampling from a given to-step sequence was
characterized by a ‘need’ term, which emphasizes the expected number of visits to a
given state (if it is never visited, it won’t offer any behavioural benefit) and a ‘gain’
term which describes the expected increase in reward following the updated policy.
During planning, states directly ahead of the animal are more likely to be visited
such that the ‘need’ term dominates, leading to forward sweeps. In contrast, when
a reward is reached the ‘gain’ associated with modifying ones behavioural policy
such that future trajectories are more likely to lead to the current goal encourage
re-sampling from the immediately recently visited states. However, evaluation of
the gain term in particular is itself a computationally intensive operation.

### 5.4 Methods

#### 5.4.1 The optimization objective

Before defining the function form of the posterior that will be the subject of the
maximization, it is instructive to first consider the notion of pairwise distance in
the case of periodic space. Since the PC locations are only encoded up to the scale
of the grid module, their absolute locations in real space may not be recoverable if
that space is larger than the grid scale. Indeed, given a nested spatial code like that
provided by multiple grid modules of different scales, the largest and smallest grid
scales will dictate the maximum range and resolution of the decoding ([Mathis et al.
(2015)]).

Therefore, the notion of ‘distance’ on the GC sheet that could be obtained by com-
paring the relative locations of the weights from two PCs actually corresponds to
to an infinite number of possible distances, corresponding to tilings of each point
outside of the fundamental domain. The likelihood function must then consider for
each pair of points these numerous possible tilings. Thus, the final posterior can be
defined as:

\[
P(X) = 2 \prod_{1 \leq i \leq n} \prod_{1 \leq j \leq n} \sum_{u,v=-\infty}^{\infty} \exp(-w_{ij}(\delta_{ij} - ||x_{u,v}^{(i)} - x_{u,v}^{(j)}||_2)^2) \cdot \prod_{1 \leq i \leq n} w_{PG}^{(i)}(X) \tag{5.8}
\]

where:
\( \chi_{u,v}^{(i)} = x_i + \lambda \begin{bmatrix} u \cdot \cos(\pi/3) \\ v \cdot \sin(\pi/3) \end{bmatrix} \) 

(5.9)

is used to simplify the notation. \( \lambda \) is the grid scale, \( W_{PC}^{(i)} \) is the vector of weights from PC \( i \) to the GCs and \( ||.||_2 \) denotes the Euclidean distance.

### 5.4.2 The sum-product algorithm

As in the previous chapter, an algorithmic solution to optimizing the landmark location beliefs is first developed. Message passing between nodes (PCs) is implemented using the sum-product algorithm [Pearl (1982)]. For a single node, an update cycle consists of two steps; a message broadcast and a belief update. However, before detailing these processes the two following definitions are reiterated for clarity:

**Belief** A probability distribution describing the possible locations of a given PC (landmark) in grid space, encoded in the PC-GC weights.

**Message** The transmission of a probability distribution from the broadcasting node to a neighbour encoding the broadcasting node’s belief over the location of the receiving node.

Firstly, at iteration \( n \) the node \( t \) integrates all messages \( m_{u \rightarrow t}(x_t) \) received from its neighbours \( u \in \Gamma_t \) with its prior self-belief \( W_t^{(0)}(x_t) \) and computes its updated self-belief:

\[
W_t^{(n)}(x_t) \propto W_t^{(0)}(x_t) \prod_{u \in \Gamma_t} m_{u \rightarrow t}^{(n)}(x_t) 
\]

(5.10)

where \( x_t \) is the position in grid space \( x \) node \( t \). Note that \( W_t(x_t) \) represents a continuous function over grid space; in reality, this function would be a discrete vector containing the weights from PC \( t \) to all GC. However, the continuous notation is used for consistency and comparison with standard definition in the literature.

Eq. 5.10 therefore represents the belief of node \( t \) over its own state (location) given all current messages from its connected neighbours in the graph. Secondly, node \( t \) broadcasts messages back to its neighbours expressing its belief over their states:

\[
m_{t \rightarrow u}(x_u) \propto \int \psi_{tu}(x_t, x_u) \cdot W_t^{(0)}(x_t) \prod_{v \in \Gamma_t \backslash u} m_{v \rightarrow t}^{(n-1)}(x_t) dx_t 
\]

\[
\propto \psi_{tu}(x_t, x_u) \frac{W_t^{(n-1)}(x_t)}{m_{u \rightarrow t}^{(n-1)}(x_t)} dx_t 
\]

(5.11)
where $v \in v \setminus \Gamma_t$ denotes the set of neighbours $v$ of $t$ that does not contain $u$, the node to which the message is being sent and the factor $\psi_{tu}$ describes the belief of node $t$ over $u$ that is generally independent of the current states of both nodes. In the current context, the factor (interaction) nodes $\phi_{tu}$ correspond to the Gaussian belief over the pairwise distance between two nodes:

$$
\psi_{tu}(x_t, x_u) = \psi_{ut}(x_u, x_t) = \sum_{u,v=-\infty}^{\infty} \exp\left(-w_{ij}(\delta_{ij} - ||\chi_{i,v} - \chi_{j,v}||)^2\right) 
$$

where $w_{ij}$ is the inverse of the variance of the measurement term and $\delta_{ij}$ the encoded pairwise distance. How these parameters could be encoded is detailed in the following sections.

### 5.4.3 Scheduling

In general, ‘synchronous’ BP computes the belief update step for each node before broadcasting all new messages in the next step in a ‘breathe in - breathe out’ fashion. However, this scheduling scheme may not be suited to distributed systems such as wireless sensor network (Costa et al. (2006); Ihler et al. (2005)) since parallel scheduling inherently relies on communication between nodes which may not necessarily be available.

In general, it is desirable that nodes be able to schedule their own updates on the basis of local information only. In addition to being more practically implementable in distributed systems, asynchronous methods have been demonstrated (Elidan et al. (2012)) to improve the rate and probability of successful convergence, while at the same time requiring fewer total update cycles.

The intuition behind this result can be understood by considering the difference in the information being propagated by a given node, as compared to the information propagated in its previous message. In synchronous BP, each node is updated in turn, irrespective of whether the messages it received at iteration $n$ disagreed with its current belief. If they did, the updated belief would be different to the belief at the previous timestep such that the messages broadcast at the current iteration would also be different, since they are conditional on the self-belief. However, if a node receives messages that do not challenge its current self-belief, its messages to its neighbours will be unchanged from the last iteration. These messages in turn will have little effect on their neighbouring nodes. Propagating redundant information, which must happen during synchronous updating, is clearly computationally undesirable and might similarly be energetically undesirable in a biological system.

In residual belief propagation (RBP; Elidan et al. (2012)), the ‘message tension’ of
each node is computed as some vector norm $||.||$ between a given node’s prior and updated beliefs. The exact form of the vector norm is not crucial. However the Jensen-Shannon divergence between the two distributions was chosen (a symmetric form of the more well known KL divergence), such that the ‘message tension’ of node $i$ at iteration $n$ is defined as:

$$T_i^n = JS(x_i^n || x_i^{n-1}) = \frac{1}{2} \left[ KL(x_i^n || m) + KL(x_i^{n-1} || m) \right]$$

(5.14)

where:

$$m = \frac{1}{2}(x_i^n + x_i^{n-1})$$

(5.15)

$$KL(p || q) = - \sum_i p_i \cdot \log \frac{q_i}{p_i}$$

(5.16)

The KL divergence can be interpreted as the information gained when the prior distribution $q$ is revised to the posterior distribution $p$. When the message tension is below a predefined threshold $T_{\text{min}}$, a node is converged and ceases from broadcasting messages. When no new messages are broadcast, the process is considered to be converged.

5.4.4 Learning the recurrent PC weights

An animal, in practice, has two methods for determining the pairwise distance between two landmarks. Firstly, a remote visual measurement of both objects could be made at respective angular bearings, from which the distance can be ‘virtually measured’ (Grisetti et al. (2010a)). Secondly, the animal might physically map the distance when walking from one landmark to the other. Both methods could be argued to have their virtues depending on the specific environmental conditions, such that an ideal mechanism might rely on both. The simulations make the simplifying assumption that both visual and odometric estimates of location incur noise in proportion to the distance, also ensuring consistency with earlier assumptions made in the PI system.

As in the previous chapter, it is assumed that PCs respond with Gaussian tuning curves to the current distance of the animal from their preferred centres of firing. To reiterate; PCs are assumed to be driven by multimodal sensory inputs, one of which is likely to be proximity to environmental boundaries mediated by BVCs (Hartley et al. (2000); Lever et al. (2009a)). Under the simplistic assumption that all PCs are uniform in their tuning width and firing rate, it can be shown that the correlation in their firing rates during random exploration is related to the distance between their receptive fields (Muller et al. (1996)). Thus, using a simple modified Hebbian learning rule:
\[
\frac{1}{\tau} \frac{dW_{PP}}{dt} = P \cdot P - W_{PP}
\] (5.17)

where \( P \) is a vector containing the firing rate of all PCs and \( W_{PP} \) is the recurrent weight matrix between. The weights can be shown to converge to:

\[
w_{ss}^{ij} = \langle p_u, p_v \rangle
\]

\[
= K \cdot \exp \left( -\frac{1}{4\sigma_{PC}^2 d_{ij}^2} \right)
\] (5.19)

where \( \sigma_{PC} \) denotes the tuning widths of the PCs (assumed equal), \( p_u \) and \( p_v \) are vectors of the firing rates of PCs \( u \) and \( v \) over time and \( \langle \cdot, \cdot \rangle \) denotes their temporal correlation. It is then possible to recover the distance \( \delta_{ij} \) by applying an appropriate transformation (assuming that the tuning width is known to the PC), where the scaling factor \( K \) can be recovered by dividing by the PC’s ‘self-weight’. The correspondence is shown in Fig. 5.4D.

The current approach marks a slight departure from traditional graph-based methods which treat each observation as an independent measurement (factor node). Instead, the proposed scheme effectively average over multiple observations and assigns the result to the same factor node. This is made possible since in the present case, the system needs only recover the most recent location, rather than the entire previous trajectory (the full vs. online SLAM distinction). This approach is also enabled by the simplified nature of the graph. Whereas SLAM in practical domains optimizes a graph whose structure may change with observations, the proposed model assumes a static graph whose nodes correspond to a known set of uniquely identifiable landmarks.

Unless stated otherwise, the connectivity between the recurrent PC graph is assumed to be all-to-all, however in larger simulations this constraint is often relaxed computational efficiency. As will be discussed in the following results section, this is a reasonable assumption for two reasons. Firstly, pruning connections according to a maximum distance threshold is practically useful since more distant connections have lower weights and thus contribute less ‘tension’ to the optimization process. A more biologically reasonable assumption however would be to assume distributed connectivity, with spatial weight profile defined by a log-normal distribution (Buzsáki and Mizuseki (2014)).

5.4.5 Initiation: The prediction error

The second major departure from traditional front/back end SLAM approaches is that the back-end optimization is not computed at each time-step. As described,
the proposed approach effectively relies on two independent methods for performing SLAM, each with differing power and computational requirements. The online method defined in the previous section is computationally cheap but brittle under high noise conditions or in complex environments. The back-end, which will henceforth be referred to as the ‘offline’ system, is computationally more expensive but can robustly infer the structure of complex environments. The combination of the online and offline systems will be referred to as the ‘dual’ system.

It is proposed here that a dual-systems approach such could confer several advantages to a resource-constrained system. According to the same logic put forward in the earlier discussion of sync-/asynchronous message scheduling, employing a computationally intensive approach to arrive at the same answer as given by a cheaper approach makes little energetic sense. Ideally, the ‘offline’ system would only be recruited when the ‘online’ system is performing poorly. A ‘prediction error’ term can therefore be defined as:

\[ E_t = H(G_t) - H(W \times P_t) \]  

(5.20)

where \( H(x) \) is the information entropy, which is small if the distribution is sharply peaked and increases otherwise. Thus, the prediction error term is positive when the inbound sensory information \( (W \times P_t; \text{Fig. 5.4E}) \) has a lower entropy than the current location estimate. Interpreted another way; the receipt of a sensory input with lower entropy than the current estimate indicates that information is being introduced to the system that is likely to be ‘truer’ that the existing information.

**Algorithm 2** Online navigation and learning with prediction error initiated offline inference

1: initialize: \( W_{P2G} \sim \mathcal{U}(0, 1); \)
2: while \( t < T \) do
3:   do_movement_update; // Eq. 4.20
4:   make_observation; // Eq. 4.23
5:   if \( E_t > E_{\text{min}} \) then // If prediction error, do offline inference
6:     while any \( T_i < T_{\text{min}} \) do
7:       \( u = \text{argmin}(T); \) // Find node with max. message tension
8:       compute_and_broadcast_message(u); // Eq. 5.12
9:     for \( t \in \text{Neighbors}(u) \) do
10:       update_belief(t); // Eq. 5.10
11:       update_message_tension(t); // Eq. 5.14
12:   else // Else, do online learning as before
13:     update_PC_GC_weights; // Eq. 4.33
14:     update_PC_PC_weights; // Eq. 5.17
15:     do_measurement_update; // Eq. 4.8
Fig. 5.4: A Convergence of the BP message passing process on a toy problem. Green and red dots indicate the true locations and initial guesses, respectively (where there are no red dots, initial guess was outside the square environment). Each square denotes the belief distribution for a PC located at the corresponding location in a square grid across the environment (total of 25 PCs), as encoded by its weights to the GC sheet (here, a square GC sheet is used as an initial prototype; the true model uses a hexagonally shaped sheet). B Illustration of the wrapped distance calculation. C Inferred static structures. When the observed pairwise relationships are open-ended (bottom-row, ‘Broken Ring’) the topology of the environment is more difficult to infer. D Example of learned vs. true pairwise distances for a network of 50 PCs. E Illustration of the prediction error term. When the incoming sensory estimate has a lower entropy than the predicted belief, an offline inference event is triggered. F Both mean entropy and mean Euclidean pairwise error decrease over successive message iterations.
5.5 Results

5.5.1 Inference on static structures

The capacity of the offline system was first tested in its ability to infer the structure of simple environments. Since the present simulations only consider a single GC scale, all simulations assumed a grid scale larger than the size of the environment such that its structure could be uniquely determined. Future work will involve simulating over several grid modules treated as local submaps (Estrada et al. (2005)).

Simulations tested inference over three different structures in a 2D environment (Fig. 5.4C). Prior to the inference process, the starting locations of each PC (the PC-GC connections) were assigned randomly according to a uniform distribution. Note that the error between the prior and actual estimates of location were much larger than would likely be encountered in full navigation simulation, but the large error was desirable here to test the inference capabilities of the system.

The recurrent PC connections were initialized by simulating a period of exploration throughout the environment. The degree of noise in the PI system was not important here, since the recurrent PC connections are formed based on the intrinsic noise in the location estimate received by each PC, which was set to $C = [1e^{-3}, 1e^{-3}]$, corresponding to a base and linear-distance term.

Firstly, the inferred pairwise PC distances recovered from the learned synaptic connections during exploration closely matched the true distances (Fig. 5.4D). Secondly, the offline system was able in almost all cases to infer the true structure of the environment (Fig. 5.4C).

Fig. 5.4A shows a visualization of the inference process over a 2D mesh with randomized initial starting locations (see Fig. 5.4C (Top) for a visualization of the inferred structure). Over several iterations, the belief distributions of each cell gradually shifted from their initial estimates to align with the true locations, reducing the pairwise error (Fig. 5.4C). Moreover, the decrease in pairwise error was accompanied by a similar decrease in the total entropy (the sum of the entropies of each PC’s belief distribution encoded in the PC-GC weights; Fig. 5.4F).

This observation emphasizes an interesting feature of the system (and conditional distributions in general), which is that the likelihood of a given hypotheses can be greater that the likelihoods of its constituent sub-hypotheses, if these sub-hypotheses are consistent with each other. This is an important feature when learning is occurring in environments with sparse observations. Later in this section, it is also argued that this data-efficiency may also be important for one-shot learning.

Secondly, the offline system was tested on a ring structure. Although seemingly a
Fig. 5.5: **A** Comparison of scheduling methods. On the toy problem, selecting the next cell to update based on the cell with lowest entropy performed almost equivalently to the *max update* method. **B** Analysis of biasing the random walk scheduling method.

simpler problem (the structure is inherently 1D), these structures are in fact less structurally stable due to the lack of cross-links. Nonetheless, the correct structure was reliably inferred (Fig. 5.4C, ‘Ring’). However, difficulties arise when the ring is cut such that the PCs at the cut ‘ends’ are not connected synaptically (Fig. 5.4C, ‘Broken ring’). In this case, the system failed to observe that the two PCs were likely near to each other in physical space.

This raises a limitation of the model in that the result of the offline inference process only affects the PC-GC weights, prompting an interesting question about the ‘ideal’ function of the system. PCs are in fact known not to fire when the animal is near their preferred firing location, but obstructed by a wall. This has typically been taken to mean that PCs are in fact only responding to sensory inputs (the sensory inputs look different from the other side of the wall). However, another interpretation is that they represent the topology of the environment (Stachenfeld et al. (2017)) rather than absolute location in space. The ability to infer synaptic connections between two PCs as a result from this offline inference process might be considered a feature of an ‘ideal’ SLAM system. However, it is unclear whether this is the case experimentally and this possibility is not explored in the current framework.

### 5.5.2 Comparing scheduling methods

Next, the effects of various scheduling methods on the convergence of the offline method were compared. Convergence was tested on the 2D square mesh as described in the previous chapter and evaluated by assessing the mean pairwise Euclidean error between the true and estimated landmark locations:
\[
\text{MSE}_{PW} = 2 \sum_{i=1:N} \sum_{j=i+1:N} \text{abs}(||x_i - x_j|| - ||\mu - \mu_j||) 
\]  

(5.21)

where \(x_i\) and \(\mu\) are the estimated and true landmark locations, respectively. The pairwise error metric in eq. \(5.21\) defines an error over the inferred structure, rather than the absolute location of the inferred landmarks. This was important, as there is no true correspondence between a landmark’s location in real space and a ‘correct’ location in GC space, rather there are only measures of relative distance between locations. For this reason, the inferred structure is only correct to an arbitrary translation, rotation or mirroring. However, in practice the structure is usually ‘anchored’ to the initial locations by the prior formed when the first landmark was observed at the animal’s starting location.

Four different scheduling methods tested. Firstly, a sequential schedule, where each cell was updated in a ‘round-robin’ fashion (Elidan et al. (2012)) such that all cells participate in the same overall number of broadcast cycles. Secondly, a max update schedule (Elidan et al. (2012)), which selects the next cell to update as the cell whose belief changed the most following the receipt of the messages from the last update cycle (described previously). Thirdly, entropy, a schedule based on choosing the cell with the highest current belief entropy. This scheduling scheme was motivated by the supposition that information should be propagated from the nodes with the most certain belief (lowest entropy). Lastly, a random walk schedule was also simulated for comparison, with a bias parameter that could be tuned to prefer short graph-hops.

As expected, the max update schedule performed most effectively, marginally winning out against the sequential schedule (Fig. 5.5A). The modest improvement is in general representative of the more significant gains that this schedule is capable of achieving (Elidan et al. (2012)). Without explicit simulation, it is likely that due to the homogeneous nature of the inference problem (i.e. the connection strengths, the initial estimates and the connectivity of each cell are all equal), each cell might indeed require similar attention. It is likely that an inhomogeneous inference task would emphasize the advantage of the max update schedule, since it would be likely in this case that specific regions of the graph would require more updating than others.

Somewhat surprisingly, the random walk approach was the worst performer, even when modulating the bias parameter such that shorter graph-hops would be preferred (Fig. 5.5B).

Interestingly, selecting a cell based on its current entropy performed nearly as well as the sequential schedule. This is notable, since the latter is somewhat more com-
putationally expensive than the former, because it requires that each cell must first update its belief in order to compute the resulting change in belief. In contrast, picking cells based on their entropy only requires assessing their current beliefs. It is unclear whether this result would hold for more complex inference problems, however the discussion is revisited in the next chapter, which explores a possible neural implementation.

5.5.3 Prediction error triggers loop closure

Next, the ‘dual’ system (online+offline) was tested on a more behaviourally relevant task. In this task, the agent navigates anti-clockwise around a curved circular 1D track (Fig. 5.6A). PCs were distributed uniformly around the track and the initial confidence in location was set as a delta function (the estimate of location represented by the firing of the GCs consisted of a single sharp peak).

The strong initial certainty meant that the place and grid cells active at the start location (0 rads) formed strong initial associations. However, as the animal navigates around the track, PI error gradually accumulates such that the confidence in locations decreases, resulting in subsequent PC-GC associations becoming weaker and less likely to correspond to their true locations.

Due to this incurred error, when the animal completes a full circle it receives a sharp input from the PCs active at the initial location. Since the current location estimate is uncertain, the entropy of the incoming sensory input is lower, causing a positive prediction error (Fig. 5.6B). Note that prediction error is negative at all other locations. The positive prediction error at the start location triggers an offline inference event.

Firstly, following the event the pairwise error in the landmark locations decreased significantly. This decrease was markedly larger than the equivalent trial using the online system only (Fig. 5.6C, 10 trials). Remarkably, continuation along the track showed that the system was able to navigate with dramatically reduced error following the event, illustrated by the flattening of rate of error decrease (Fig. 5.6C). Accordingly, a second complete lap of the track caused a much smaller prediction error (Fig. 5.6B).

Revisiting an earlier discussion, it is emphasized that the learning rate of this system is much faster than can be expected by a network employing simple Hebbian learning, instead resembling a one-shot learning process. Moreover, the results were obtained following only a single observation cycle. These results are contingent on the fact that the animal was effectively able to construct a hypothesis from the observations and movement that it perceived that were self-consistent. In this, trial the PI noise is again set to relatively high levels such that animal was ‘surprised’ to arrive back at the start location when it had in fact perceived a different trajec-
However, the result would be the same had the animal navigated under low PI noise; in this case, the expected sensory input would not be corrective but instead reinforcing. That is to say; confirmation of an initial belief by sensory input with lower entropy will have the effect of strengthening the belief but not changing its mean.

5.5.4 Hippocampal replay as offline inference

Replay sequences following loop closure on a 1D track

Next, the sequences of message passing that arose from the asynchronous scheduling strategy were analyzed in greater detail. Fig. 5.6A shows typical examples of sequences following the positive prediction error triggered upon first completion of a loop on the 1D ring, for different levels of observations noise (C). Notably, the sequence of message broadcasts is seen to initially propagate backwards along the track from the animal’s current position, before beginning a new sequence at a remote location in the graph which propagates back to the start. These sequences are followed by several smaller sequences, each of which tend to propagate in short sequences along the PC graph. These sequences bear a striking resemblance to the spatially ordered sequences of PC reactivations observed in the hippocampus (Foster and Wilson (2006b); Diba and Buzsáki (2007)).

The sequences did not reflect random hops through the landmark graph. Secondly, the sequences did not reflect constraints of local synaptic connections, since nodes were connected in an all to all manner. Moreover, the ‘hopping’ from one part of the graph to another (reflecting the end and start of sequences, respectively) showed clearly that the sequences did not purely reflect the stronger synaptic weights between neighbouring cells.

Instead, the sequences represent the transmission of information around the graph. Due to the imposed threshold, PCs only transmitted messages when their beliefs were significantly changed, which could only occur in response to receiving new messages from their neighbours. Since the confidence of statistical relationship between neighbouring cells decreased with distance, cells were more likely to be influenced by messages from their nearby neighbours. Thus, sequences were likely to proceed in short ‘hops’. However, this was not the only possibility, as evidenced by larger ‘hops’. It is likely that larger ‘hops’ (which bypass neighbouring cells) imply that the graph location at the end of the update sequence is not changed significantly by the new information being propagated. Thus, the next PC to fire will be the PC whose ‘surprise’ is greatest, which may be located in unrelated location of the graph. It might then be expected that subsequent sequences (i.e. not including the initial sequence) would be less ‘sequency’.

To explore this hypothesis, sequences both within and across successive offline infer-
Fig. 5.6: A The loop-closure task, where blue circles indicate uniformly distributed place fields around the circular track. B Prediction error over time. When the agent returns to the starting location \((2\pi)\), it receives a positive prediction error from the strong sensory input that was learned at the beginning of the trial. The prediction error is diminished over successive laps, reflecting increased familiarity due to learning. C Offline inference as one-shot learning. Mean pairwise error between the locations of the estimated place fields is instantaneously reduced following an offline inference event as compared to the slow reduction with purely Hebbian learning. D Typical PC reactivation sequences as a function of the noise in the pairwise PC measurements. Noisier pairwise measurement cause information to propagate more gradually through the graph and reduces the effect of messages on neighbouring nodes. E Histogram of forward and backwards sequences, where positive = anti-clockwise. F Sequence metrics as a function of the pairwise measurement confidence. Pairwise confidence can also be seen as comparable to the ‘convergence’ of the structure, which would occur with learning over time. Mean sequence length is broadly inversely correlated with the hop distance and tortuosity. Together, these metrics reflect the fact that in novelty, sequences will be long, smooth and unbroken, whereas with experience (or confidence) sequences will tend to be shorter, may reverse directionality frequently and ‘hop’ between different locations in the place cell graph.
ence events were analyzed. A single sequence is denoted by the set \( S = (s_1, s_2, ..., s_N) \) where \( N \) is the length of the sequence and \( s_i \in 1, ..., N_{PC} \) is an integer denoting the index of the PC that was active at position \( i \) in the sequence. Since the simulation was defined on a circular track, four descriptive metrics were devised, operating in angular coordinates:

\[
L = N \quad \text{Sequence length (5.22)}
\]

\[
D = |\theta_{s_N} - \theta_{s_1}|_c \cdot \text{sgn}(|\theta_{s_N} - \theta_{s_1}|_c) \quad \text{Signed distance (5.23)}
\]

\[
H = \frac{1}{N-1} \sum_{i=2}^{N} \text{abs}(|\theta_{s_i} - \theta_{s_{i-1}}|_c) \quad \text{Mean hop distance (5.24)}
\]

\[
T = \frac{1}{N-2} \sum_{i=2}^{N} \text{abs}(|\theta_{s_{i+1}} - \theta_{s_i}|_c - |\theta_{s_i} - \theta_{s_{i-1}}|_c) \quad \text{Tortuosity (5.25)}
\]

where \( \theta_{s_i} \) denotes the location of PC \( s_i \) in real space. The length metric measured the number of elements in the sequence. The signed distance metric measured the total distance travelled in angular coordinates in the anticlockwise (+ve) and clockwise (-ve) directions respectively. The mean hop distance measures the mean length of transition between subsequent activations in terms of physical locations in space and can be interpreted as a measure of propagation speed. The tortuosity metric measures the ‘straightness’ of the sequence trajectory. Sequences with tortuosity \( T = 1 \) would be unidirectional, whereas \( T < 1 \) would denote a sequence that took a ‘tortuous’ (winding) path from start to finish.

Firstly, the analysis considered whether it was possible to quantify the structure of the sequences as a function of the information being propagated through the graph. Initially, it was hypothesized that more salient or ‘surprising’ information would propagate more quickly through the graph. This was analyzed by comparing the mean hop speed (a measure of speed) against the variance in the pairwise PC measurements (Fig. 5.6C, Middle). The analysis confirmed a strong positive correlation.

Variance in the pairwise error measurements strongly affected the speed of propagation, as measured by the hop-distance (Fig. 5.6F, Middle). When the pairwise measurements were more confident (less noise), sequences tended to skip neighbouring cells and so propagate more quickly. This suggested that a message from the broadcasting PC tended to influence PCs over a greater range. Consider the following scenario:

1. Cells C and D receive a message from A. Cell C is nearer to A an so is updated slightly more than cell D.
2. Cell C is the next to broadcast message, having updated its belief following the receipt of the message from A. C broadcast its message to D and E.

3. The message being broadcast from C reflects new information from A. However, this information was also received and incorporated by D. Thus, D only revises its belief to a small degree following the message from C.

4. Conversely, cell E receives little of the information from A’s message and thus revises its belief upon receipt of C’s message. Thus, E is the next cell to broadcast following C, skipping D. The sequence has thus far proceed A, C, E.

This skipping effect marked the separation of the entire replay event (Fig. 5.6D) into several subsequences when the hop distance exceeded a threshold ($H_{\text{max}} = 5$). Thus, the above result was also confirmed in an analysis of the average sequence length (Fig. 5.6F, Left). The sequence length was inversely related to the hop-distance. Thus, replay events with low measurement confidence (high variance) were characterised by long unbroken sequences (Fig. 5.6D, Left). The skipping effect was also captured in the tortuosity metric, showing that sequences got broadly less direct as the measurement variance decreased (Fig. 5.6D, Right; F, Right).

Secondly, since the agent navigated with monotonic speed anticlockwise around the track, sequences proceeding in the anticlockwise and clockwise directions could be interpreted as forward and reverse ‘replay’ events, respectively (Fig. 5.6B). The proportion of forward and reverse events were approximately normally distributed with mean distance $D = 0$, although initial events tended to proceed away from the current location.

### 5.6 A neural model

The previous section introduced a model for offline structural inference based on message-passing through a graph. It was demonstrated that by scheduling messages using information-theoretic principles, graph convergence was faster, more efficient and less energetically costly than naive round-robin schedules. Moreover, the message schedules were compared to those generated during PC replay, suggesting that these reactivations might serve to propagate information throughout the network so as to converge on a consistent hypothesis about the structure of the environment.

Despite its appealing functional interpretation and explanatory power, the previous algorithmic implementation of BP does not however constitute a biologically plausible mechanism for how this process might occur in the HPC, although the distributed nature and low per-node computational requirements of the algorithm suggests that a plausible implementation might be possible. This section presents one such possible solution, adhering to the constraints of the biological circuitry outlined previously. The proposed mechanism relies on coincidence detection between
PC spikes and a simultaneous wave of activity that spreads along the grid sheet and makes several experimentally testable predictions.

5.6.1 Message Propagation

A message broadcast is initiated by the firing of a spike from the broadcasting PC. This spike is communicated to all neighbouring PCs with a conduction delay that is assumed to be inversely proportional to the connection strength (linearly proportional to the pairwise distance).

In parallel, the same spike from the broadcasting PC drives activity in the GC sheet (Fig. 5.7B-D). The instantaneous activity on the GC sheet represents the current belief of the broadcasting PC’s location in GC space, since the spike is modulated by the PC to GC weights learned during online exploration. This activity is assumed to propagate radially outwards at a constant speed from the initial activation site, whilst accumulating noise that is proportional to the distance travelled.

The development of this activity over time manifests as a travelling wave across the GC sheet (Fig. 5.7E, G). Mathematically, this wave describes a process of PI from the initial point emanating radially in all directions (since the PC-PC connections encode distance and not bearing).

The process is illustrated in 1D in Fig. 5.7B. To summarize, a broadcasting PC \( P_B \) sends a spike to a receiving PC \( P_R \). When \( P_R \) fires, it will modify its associations to whichever GCs are firing at that instant. If the distance between the encodings of \( P_B \) and \( P_G \) on the GC sheet agree with the distance encoded in the weight \( w_{rb} \), the spike and waves will arrive simultaneously such that no change in belief is triggered.

5.6.2 Belief Updates

The arriving spikes from the broadcasting PCs are assumed to be insufficient to cause spiking in the receiving PCs. However, the subthreshold activation allows a learning update to occur such that the current weights of the receiving PC (representing the current belief) are pushed towards the current activity of the GCs:

\[
W_i^{(n)} = W_i^{(n-1)} \cdot G_t
\]

i.e. the new belief is simply the product of the current GC activity (the message from the broadcasting PC) and the prior belief (encoded by the weights). Thus, if the spike arrives at the receiving PC at the same time as the GC wave reaches the location at which the PC was previously encoded, there will be relatively little change in the weights (Fig. 5.7B). Conversely, if the spike travels faster or slower, the belief of the receiving PC will be revised to be closer or further from the origin of the wave, respectively (Fig. 5.7C, D).
Finally, the difference between the new and previous beliefs, which is represented by the total change in PC-GC weights is calculated in a similar vein to the prediction error term, i.e. the KL divergence between the two terms. This mechanism could plausibly be related to the build up of some learning related neuromodulator.

This buildup is equivalent to the message tension described earlier in the algorithmic BP solution. Thus, if the learning event produces a significant message tension, the receiving cell will also broadcast its own spike. If the incoming message is not sufficiently different to the current belief, learning still occurs due to the subthreshold input, but no spike is broadcast.

Importantly, the PC-PC weights are not updated during the offline inference process, only during online learning (eq. 5.17). These observations are independent of the current estimate of position such that their encoded pairwise landmark estimates decrease in error over time. Thus, they are the ’ground truth’ to which the PC-GC weights must be calibrated.

_Travelling waves in neural media_

In simulations, propagation of this wave is simulated explicitly by calculating the true wrapped distribution at each time-step, however it is known that various neural media can support travelling waves (Ermentrout and Kleinfeld (2001); Muller et al. (2018)).

Neural oscillations have long been though to be crucial to neural processing. Their prevalence across brain regions and species boundaries reinforce this notion, suggesting that oscillatory activity may underly broad and generalized computational principles.

Most of the proposed roles of oscillations are related to their synchronizing properties. Macroscopic oscillations may synchronize the activity between distinct brain regions which may be functionally distinct, allowing fine-grained interactions that might allow complex processing such as the coupling between V1 and V2 areas proposed for the binding of visual features into a perceptual unit (Von der Malsburg and Schneider (1986)). Theta-nested gamma oscillations may be important for the temporal ordering of sequences and episodic memories, facilitating recall or learning by binding discrete events on synaptic plasticity relevant timescales (Lisman and Idiart (1995)). PCs in the HPC are known to participate in phase precession (O’Keefe and Recce (1993)), where firing occurs at successively earlier phases of the theta cycle as the animal traverse their associated place fields. In general, neurons have been found to be more sensitive to dendritic depolarizations that occur close in time, suggesting that information might be more effectively transmitted between brain regions if the activity in the broadcasting region is synchronized (Swadlow et al. (1998); Harris et al. (2003); Buzsáki and Draguhn (2004)).
Oscillations are characterized by rhythmic fluctuations in the spiking activity of participating neurons. Most functional hypotheses have considered the precise temporal alignment of distinct regions. However, although synchrony must be frequency coupled it may nonetheless be offset in phase, defining travelling waves of oscillatory (Muller et al. (2018)). Sleep spindles have been demonstrated to propagate both radially from a point source and in a spiral with preferred direction across the cortex (Muller et al. (2016)).

In contrast to macroscopic waves, mesoscopic waves have been observed that propagate over smaller distances, typically being confined by anatomical boundaries. In V1 and V2, mesoscopic waves evoked simultaneously travel in parallel across their respective retinotopic maps, allowing the possible integration of simultaneously activated information (Muller et al. (2016)). Travelling waves’ propagation speed has been found to be extremely reliable and are broadly consistent with axonal conduction speeds (Girard et al. (2001)).

Outside of their synchronizing properties, several functional roles have been speculated for travelling waves. Dense waves, which interact strongly could form the basis for logical computations such as AND or OR gates (Muller et al. (2018)). Weakly interacting waves may allow multiple historic stimuli to be preserved and retrieved through their slowly propagating activity (Perrard et al. (2016)). However, these theories are in their comparative infancy in neuroscience domains since the exact characterization of travelling waves has relied on comparatively modern multichannel electrode technologies and new analysis techniques (Muller et al. (2018)).

In contrast, the mechanistic bases of travelling waves have been well studied (Ermentrout and Kleinfeld (2001)). Much of the theory is grounded in classical physics works, the main difference residing in the fact that neurons constitute an active rather than passive medium. Early work focussed on continuum approximations based on solutions of simplified and biologically motivated systems of ordinary differential equations (Wilson and Cowan (1972)) but have progressed with the advent of modern computing systems to the simulation of entire populations of spiking neurons.

Broadly, travelling waves can be induced in media with local connectivity such that an initial stimulus gradually propagates activity radially outward from its initial location. Travelling pulses (Amari (1977b)) can be differentiated from travelling waves in that they are characterized by a moving packet of activity. There is therefore some ambiguity in the discussion of travelling waves in the literature; travelling waves often refer to travelling pulses, but should specifically refer to activity patterns that spread outward such that all neurons within the radial boundary are active, as opposed to the former where only neurons at the travelling front are active.
Implementing the BP mechanism in neural media requires a travelling pulse solution. Most media that are able to satisfy travelling waves are also able to support travelling pulses. Typically, a pulse solution is formed by assuming synaptic depression or long rebound time, such that neurons are only transiently active. In this way, freshly recruited neurons at the front of the wave are active but quickly become inactive as the wave front passes such that only neurons at the front are ever active.

The main feature of all existing travelling pulse solutions is the exact preservation of the initial stimulus pattern as it is shifted through the neural field. However, the proposed solution also requires that the initial stimulus shape be broadened to represent accumulating uncertainty about location. Since the present study is not overly concerned with whether the biophysical properties of the mEC is capable of supporting travelling pulses (although see [Hasselmo (2014)], which suggests that travelling waves may be supported by mEC and that their propagation speed may be controlled by HCN dynamics), a simplified model of wave propagation was preferred, which focuses on intuitive demonstrative power rather than exact biophysical realism. The proposed model is based on the form of a simple mechanical wave such as can be used to describe oscillations in water:

\[
\frac{dv^2}{dt^2} = c^2 \nabla^2 \cdot v
\]  

where \( c \) is the speed of wave propagation (5.7H). The \( \nabla^2 \) term would normally represent the spatial Laplacian \( \nabla = (\frac{d}{dx}, \frac{d}{dy}) \) when modelling physical matter. However, the discrete Laplacian can effectively be treated as a filter:

\[
\nabla^2 = \begin{bmatrix} 0 & 1 & 0 \\ 1 & -4 & 1 \\ 0 & 1 & 0 \end{bmatrix}
\]  

which computes the 2D spatial differential (this form corresponds to a 2D finite difference scheme). In physical matter, this form would imply that particles of matter are only influenced by their immediate neighbours. However, here the notion of the Laplacian is generalized to a 2D Gaussian with variance equal to the PI noise.

Although analytical proof is not provided, it was found empirically that simulation of this form broadly matched the propagation of the true probability distribution (5.7G). Due to the modified filter, the speed of the wave was found to be slower than the theoretical case, but was easily accommodated by scaling the wave speed parameter \( c = c' \cdot \alpha \), where \( c' \) was the desired speed of the wave and \( \alpha \approx 0.3 \).

In addition to being accurate propagation speed, the wave approximation of the ex-
panding distribution matched the desired broadening of the expanding distribution (Fig. 5.7G). Although the approximate form displayed some transient secondary and tertiary wave components, it is emphasized that a more closely matching solution could likely be found with suitable modification of the basic form.

5.6.3 Results

*Equivalence of Scheduling*

If only a single update cycle is allowed to occur at any one time and the PC with highest message tension is chosen to broadcast next in the sequence, the neural mechanism outlined is almost equivalent to the algorithmic BP solution. However, the learning rate in 5.26 is slightly different to the true update in 5.10, since the effect of the previous message is not erased nor is the prior belief maintained throughout successive update cycles. In practice, the two algorithms perform almost equivalently on the same toy task (Fig. 5.7F).

5.7 Discussion

5.7.1 Summary

In summary, this chapter proposed an augmentation to the online learning system that allows inference over complex learning environments. This offline system relies on the assumption that the error in successive measurements between pairs of landmarks decrease over time and are not subject to the biases introduced by active navigation.

It was proposed that pairwise distances can be represented by an offset Gaussian distribution, allowing a compact representation of the distribution to be stored in the pairwise synaptic PC connections. If measurements are assumed to be less certain in proportion to the distance, the entire distribution may be efficiently encoded in the strength of the PC-PC synapse. This assumption of distance dependent noise is not explicitly necessary; pairwise measurements could be assumed to have the same noise, independent of distance, in which case only the means (pairwise distance estimates $\delta_{ij}$) would need to be encoded. However, distance proportional noise is a realistic assumption and so would likely improve the inferential ability of the system by correctly down-weighting the effects of messages from neighbours representing PCs with more distant place fields.

A modified Hebbian learning rule was proposed to allow these connections to be learned and a transformation defined to allow the encoded weights to be implemented in neural processing. This transformation would be performed by each PC and is contingent on each cell having an intrinsic knowledge of its own firing variability.
In the proposed model, structural inference is assumed to be performed via a message passing process. It is first shown that asynchronous scheduling is superior to synchronous scheduling both in terms of convergence probability and rate but also in terms of energetic cost. For a neural system constrained by limited neural hardware, the latter may be an important factor.

Moreover, it is demonstrated that asynchronous scheduling produces PC reactivations that bear similarity to those observed during hippocampal replay. The model therefore interprets replay as a process of propagating information through a graph representing the structure of the animal’s environment. The model produced both backward and forward sequences in equal measure, though more work is required to analyse the observed sequences in broader behavioural contexts.

The proposed model offers a novel functional perspective on the role of hippocampal reactivations. Unlike theories based on RL, reactivations are not based on reward nor on planning. However, the model predicts that the impairing of sharp-wave ripples (and therefore replay) should impair learning (Girardeau et al. (2009)). To my knowledge, it is also the only existing model describing the interaction of PCs an GCs during replay. Moreover, assuming that the GC wave is initiated by PC activity, the model also suggests that replay can occur in GCs independently (O’Neill et al. (2017)) if the ‘messages’ do not cause a sufficient change in the belief of the receiving PCs to cause them to spike (broadcast their updated beliefs). Nonetheless, the proposed model is consistent with the idea that replay events are initiated in the HPC (lafsdttir et al. (2016)).

In contrast to RL predictions, it has been observed that replayed trajectories do not necessarily reflect trajectories that are in active use or have been recently visited (Gupta et al. (2010)). Although more work is required to explore the present results in open environments, the theory suggests that trajectories should be replayed based on their dissonance with the rest of the map, such that new information should be propagated to states (PCs) regardless of their roles in planning.

There are however some problems with the model, firstly that it does not make strong predictions about the role of forward replay, other than demonstrating that they may also contribute to consolidation. The second line of future investigation is to explore in more detail the effect of repeated replays on the their sequence properties. Initial analysis (Fig. 5.6F) suggest that replays should become more ‘hoppy’ as the convergence of the graph increases, which implies an increase in absolute speed (in terms of number of ‘hops’ and therefore time taken to go from A to B). In contrast, the first awake replay experiment showed that replay sequences on a linear track slowed over time, recruiting more spikes per PC and more PCs in total to the sequence. The latter finding suggests that a more complex mechanism
is in play, which is not modelled by the present study. Nonetheless, the model reproduces the ‘hovering’ or ‘jumpy’ nature of real replay sequences (Pfeiffer and Foster (2015)), predicting that traversals through the PC graph are not determined purely by adjacency in synaptic connections.

The current work thus argues that replay may imbue the brain with the ability to perform one-shot learning when the information contained in the system is self-consistent. Accordingly, replays are known to occur after single laps of a linear track (Foster and Wilson (2006a)). Unlike some existing SLAM models where the back-end is in constant operation, the ‘back-end’ of the current system is only invoked when the ‘front-end’ online system is found to be deficient. This deficiency is quantified in terms of prediction error, defined as the K-L divergence between the predicted and incoming sensory input. Functionally, the current proposal makes energetic and computational sense, since offline inference requires the re-activation of non-local PCs, which might preclude them from being used for other purposes. In contrast, the online system only learns using the currently active PCs.

Prediction errors are assumed to be indicative of new and useful information entering the system and trigger offline inference events. In the context of hippocampal replay, prediction errors could therefore be considered as analogous to sharp wave-ripples, which are thought to trigger replay. Thus, the proposal is that prediction errors should trigger sharp wave-ripples.

Prediction errors should occur when the animal reaches a location that conflicts with its current estimate of location. To analyze this circumstance, simulations considered a task whereby the agent navigates around a 1D circular track under high noise conditions. When the agent arrives back at the starting location, strong sensory input from PCs causes a prediction error, triggering an offline inference event. The pairwise measurements between PCs on the ring are relatively accurate at short distances and are consistent in the sense that a hypothesis about their global structure (a ring) describes the pairwise measurements and the perceived trajectory well. These factors allow the agent to learn much faster than it would if it were to rely purely on the online system. It is predicted that an experiment of this kind should result in place field shifts following replay events.

Lastly, the algorithmic proposal is complemented by a biophysically realistic model that is comparable in performance to the algorithmic implementation. The model predicts that activity propagating on the GC sheet should coincide with concurrent spikes broadcast in the PC network, if the pairwise PC-PC measurements are consistent with their relative encoding locations in grid space. When these two independent encodings of distance are different, differences in the relative transmission times of the $P_B \rightarrow P_R$ spike and the GC wave would cause synaptic activity such as
to push the PC-GC weights to align with the pairwise distance estimate encoded in the PC-PC weights.

This neural implementation however relies on the assumption that the speed of the propagation of spikes along PC-PC synapses is proportional to the strength. Broadly speaking, this assumption might be plausible if the synaptic strength were considered as analogous to electrical conductance. Although this mechanism is not simulated explicitly, a larger conductance might allow a faster build-up of sub-threshold potential at the receiving dendrites.
Fig. 5.7: A Experimental evidence for travelling waves in the brain. (Left) The hippocampal theta wave is a travelling wave (Lubenov and Siapas (2009)). (Middle, Right) Radial travelling waves in V1 and V2 (Slovin et al. (2002), Muller et al. (2016)). B-D Illustration of the neural BP mechanism. The broadcasting PC sends two simultaneous spikes. The first is broadcast to its neighbouring PCs. The second is broadcast to the GC sheet via the PC-GC connections learned during online exploration, initiating a wave of activity that propagates radially outwards. Here, the time of the PC spike and GC sheet wave is color coded. B The PC spike reaches its neighbour at the same time as the GC wave reaches the location at which the receiving PC was previously encoded (GC 7), so the weights do not change. C The PC spike travels more quickly than the GC wave, causing the receiving PC to revise its belief over its location by updating its weights (from location 7 to 5). D The same as previously, except that the spike moves more slowly than the wave. E Example of waves propagating in 2D over the GC sheet. Note that the waves wrap at the edges and may interact when they return. F The neural and algorithmic algorithms perform equivalently on a toy task. G Equivalence of algorithmically generated travelling wave and neurally plausible solution. H Effect of wave speed parameter on true wave speed. ‘Stickiness’ at low velocities is likely a numerical issue. Note that the GC wave needs only ever to travel at a fixed speed.
6. GRID CELL ANALYSIS

I thank the Moser lab for kindly allowing access to their dataset.

6.1 Introduction

Almost all previous modelling and analysis of GC firing patterns is based on the assumption that the ‘ideal’ pattern is that of a uniform triangular lattice, with the exception of the work of Stensola et al. (2015). Research tends to publish the ‘best’ examples of recorded GCs, which by the definition of the commonly used grid score favours regularity.

The first and most pervasive ‘grid score’ was introduced by Sargolini (2006) (see Appendix) and is based on an assessment of the six-fold rotational symmetry of the rate map’s spatial autocorrelogram (SAC). From the SAC a circular area containing the central peak and its six nearest surrounding peaks is extracted, which can be correlated with rotated versions of itself to assess rotational symmetries. The gridness score is defined as the minimum of the correlation at 60° and 120° rotations minus the maximum of the correlation at 30°, 90° and 150° rotations. A perfect grid score is achieved when the circular area is perfectly correlated at one of the 60° rotations (corr = 1) and anticorrelated at the 30° rotations (corr = −1) such that $G = 1 - (-1) = 2$. Extensions to this method include an “expanding gridness score” which gradually expands the radius of the inner circle and selects the maximum gridness score (Langston et al. 2010), an “elliptical gridness score” which allows the inner area to be elliptical rather than circular (Brandon et al. 2011; Stensola et al. 2015) and an “expanding elliptical gridness score” which combines aspects of both (Killian et al. 2012).

The inclusion of an ellipticity measure was the first attempt to recognise that the GC pattern can depart from perfect regularity while still being recognised as a ‘grid pattern’. However, even an elliptical gridness score only accounts for a limited set of possible distortions to the grid pattern, namely shearing and scaling. Both are examples of affine transformations, which preserve points, straight lines and planes. Following an affine transformation, sets of parallel lines will remain parallel and the ratios between sets of points on the same line will also remain the same. Affine
transformations can be represented by 2D transformation matrices, which may be combined with a linear coordinate shift to realign the locus of the transformation.

Importantly, affine transformations are applied uniformly to a pattern, thus ignoring the possibility of local distortion effects. Stensola et al. (2015) showed that there can in fact be significant variation in the local properties of the grid pattern. This was demonstrated by separating the global SAC into smaller sections and applying an elliptical gridness measure to each (Fig. 6.1A). The authors found that the grid pattern was significantly more elliptical near the corners and edges of an environment and that the effect was more prevalent in larger environments (Stensola et al. 2015).

However, their analysis only quantified shearing transformations and scaling to the grid patterns. On one hand, their model based analysis allowed the authors to elegantly quantify the distortions in terms of relatable parameters (magnitude and locale of shearing), providing a convenient starting point for reasoning about the possible mechanistic explanations such as those presented earlier in this thesis. On the other hand, it is unlikely that all distortions to the grid pattern can be characterized in such simple terms. Moreover, an arbitrary compartmentalization of the grid pattern is not an elegant description of the local variation in distortion and does not allow the possibility of exploring the possibility of single, continuous but non-linear transformations applied globally.

Metrics computed from firing rate maps assume the presence of measurable peaks at the location of each of the ‘true’ grid pattern’s vertices. This is not necessarily the case; firing rates are known to vary significantly from field to field allowing the possibility that a field’s firing rate might not exceed the detection threshold (Fig. 6.1G). In the case of significant distortions, multiple fields might overlap so as to appear as a single field. Autocorrelogram based analyses mitigate this problem to some extent (since a single missing field only contributes in part to the global correlation) but average out the properties of the grid pattern.

Throughout this thesis, the ‘ideal’ grid pattern was assumed to be uniformly hexagonal and departures from this regularity were assumed to be caused by various subsequent distortive processes. This assumption is not necessarily justified in the light of modelling approaches (Dordek et al. 2015a; Stachenfeld et al. 2014) based on unsupervised learning. Although under certain conditions the resultant patterns can be hexagonal, the more general conclusion from these studies was that the grid pattern is usually periodic in some form, but not necessarily hexagonal or spatially uniform (Fig. 6.1B). Thus, an interesting question is whether experimentally observed grid patterns can be best described by distortions applied to a base uniform pattern, or by a non-hexagonal base pattern.
This chapter introduces a novel method for analyzing the local properties of grid patterns. The analysis makes the implicit assumption that the ‘latent grid pattern’ (i.e. the ideal or intended grid pattern) is distorted by environmental conditions to produce the observed grid pattern, which is assumed to be uniformly hexagonal.

To remain as agnostic to the form of these distortions as possible, analysis is conducted by computing properties of a hexagonal mesh fitted to the peaks of a ratemap, where each node is connected to exactly six neighbours. Firstly, it is demonstrated that the aforementioned metrics can be elegantly computed locally based on each sub-triangle (three nodes) of the mesh. Secondly, it is shown that the assumption of latent hexagonality can help to isolate firing fields with subthreshold firing fields, or which may otherwise overlap indistinguishably from nearby fields.

Earlier work in this thesis was concerned with determining the function and mechanisms whereby distortions might arise in the grid pattern. For the most part, these distortions were assumed to be characterized by a uniform shearing transformation applied across the grid pattern \( \text{[Stensola et al. (2015)]} \). However, a closer inspection of the data suggests that this description may be overly simplistic, or at least that there is likely to be significant variation in the distortive processes at play. Chapter 4 explored a model of these distortive processes whereby nonuniformity in the density and/or firing rate of place fields can warp the grid field, reproducing a shearing transformation for a specific density function. However, the model suggests a more general mechanism that could produce more arbitrary forms of distortion.

The first aim of this chapter is therefore to attempt to explore further the reported distortions, asking whether a uniform shearing process is indeed a good description. The analyses presented in the following sections analyses suggest that there is significant non-uniformity in the local properties of the grid pattern, suggesting a more complex mechanism of distortion. Lastly, the analyses suggest that while the overall effect might resemble that of a distortion, this process may in fact arise from a combination of non-linear distortive effects.

Analysis is performed on a dataset of 957 cells \( \text{[Stensola et al. (2012)]} \), which were recorded in a series of square boxes with dimensions of 1\( m^2 \), 1.1\( m^2 \), 1.5\( m^2 \) and 2.2\( m^2 \) \( (N_{cell} = [144, 25, 562, 226], \) respectively). In the following analyses, only the 1\( m^2 \), 1.5\( m^2 \) and 2.2\( m^2 \) boxes are considered, since there were not enough cells to adequately describe results from the 1.1\( m^2 \) box.

\(^1\) Dataset obtained through personal communication with the authors.
6.2 Methods

6.2.1 Fitting the mesh

The mesh energy function

The procedure for fitting the hexagonal mesh is based on the dual aims of aligning nodes with areas with high firing rates (the putative grid fields) and a minimization of the ‘tension’ in the edges between nodes (a prior belief over the structure of the pattern).

Before the fitting procedure, each ratemap is first smoothed by convolving with a boxcar filter of width \( [5 \times 5] \), ignoring the effect of NaNs. Each fit was manually checked following the optimization procedure and manually corrected in cases where the solver had converged on a clearly suboptimal solution.

Firstly, a candidate uniform mesh is generated using the scale and orientation as extracted via standard methods from the SAC. The nodes of the proposed mesh extend beyond the boundaries of the ratemap to allow for the possibility of contraction during the optimization stage. The optimization stage iteratively refines the mesh to minimize the following energy function:

\[
E = - \sum_{i=1}^{N} g \cdot f(x_i) + \sum_{i,j=1}^{N} K \cdot (D_{ij}(X) - D_{ij}^0(X))^2 \sum_{i,j}^{N} K \cdot S_{ij} \quad (6.1)
\]

The first sum defines the total ‘gravitational’ potential of the nodes where \( f(x_i) \) is the value of the firing rate map at position \( x_i \). In the absence of any other terms, optimization would cause the nodes to settle at local maxima (c.f. negative sign) in the rate map.

The second summation represents the total mesh tension defined over all edges, where \( D_{ij}(X) = ||x_i - x_j|| \) is the Euclidean edge length between connecting nodes \( i \) and \( j \), \( D_{ij}^0(X) \) are the preferred edge lengths and \( K \) is a binary matrix of node connectivities. The third term is a local smoothness constraint, discussed below.

Local scale and smoothness constraints

On first implementing the fitting process, each preferred edge length \( D_{ij}^0(X) \) was assumed to be a global constant equal to the scale inferred from the coarse initial parametrization. However, it was found that several of the grid patterns appeared to display local variations in the grid scale. The preferred edge length was therefore allowed to vary locally, with the preferred length of a given edge defined by the mean.

\[\text{See Chapter 5 for a mathematically related formalism describing pairwise measurements and prior beliefs in a network of PCs.}\]
of the edges contained in the two adjacent hexagons to which the edge contributes (Fig. 6.1D). This can be expressed mathematically as:

\[
D_{ij}^0(X) = \frac{1}{|E_i \cup E_j|} \sum_{(u,v) \in (E_i \cup E_j)^2} D_{uv}(X)
\]  

(6.2)

where \(E_i\) is the set of edges connected to node \(i\) and \(|\cdot|\) is the cardinality (length) of a set. Secondly, a local smoothness constraint was also imposed on each edge, penalising the dot product between an edge and each of its leading and trailing edges (a triplet of edges; Fig. 6.1C). This constraint is described mathematically as:

\[
S_{ij} = (1 - |\cos(\theta_{E_{ij}} - \theta_{E_{ij}^-})|) + (1 - |\cos(\theta_{E_{ij}} - \theta_{E_{ij}^+})|)
\]  

(6.3)

\[
= (1 - |e_{ij} \cdot e_{ij}^+|) + (1 - |e_{ij} \cdot e_{ij}^-|)
\]  

(6.4)

where each (fully connected) edge \(E_{ij}\) has two adjacent edges \(E_{ij}^+/\) on the same contour line (6.1E) and each of the triplet of edges has an angle \(\theta\). \(e_{ij}\) is the unit vector corresponding to the edge between two nodes \(x_i\) and \(x_j\). In addition to allowing the model to correctly account for the observed grid pattern, enforcing local edge length and angle consistency allowed the fitting procedure to estimate the positions of firing fields lying outside of the environmental boundaries. If the preferred edge lengths were assumed constant, local contraction near the boundaries would cause a jump back to the original scale resulting from estimated fields outside the boundaries.

Estimating the positions of fields outside the boundary could be considered unreasonable. However, as will be discussed there is frequently interesting variation especially near the edges and corners of the environment and so being able to estimate descriptive metrics in these regions is important. The most common case in which the proposed procedure is important is when there is a clear field near to the edge of the boundary, but its is unclear as to where the centre of the fields lies. Biasing the fitting towards the edges of these fields would artificially produce compression at the edges of the borders (which may in fact be present in the data).

To circumvent this issue, an extrapolation procedure was applied to ‘extend’ the ratemaps outside the boundaries of the box. If the firing rate of a field is increasing as it crosses the edge, the gradient will be extrapolated outside the border. Conversely, if the gradient is decreasing (i.e. if it looks like the peak firing field does indeed lie within the borders) the region outside of the boundary will also reflect this behaviour.
The final fitted location of nodes outside the boundary are therefore as unbiased as possible by edge effects. However, the local edge length consistency also enforces the assumption that the distortion pattern varies smoothly (e.g. the scale would not jump across the boundary).

### 6.2.2 Clique metrics

Given the fitted triangular mesh, analysis is performed by computing various geometrical properties of the 3-cliques $C$ of this mesh (triangles). A 3-clique is defined as a set of nodes within which each node is adjacent. In the case of a hexagonal mesh, the 3-cliques equate simply to the distinct triangles. Thus, a given (fully connected) edge might be analysed in the context of the two cliques to which it belongs. The geometrical metrics are introduced in the next section, however each clique has a unique centroid, which is used as its 'location' for analyses purposes.

### 6.3 Results

#### 6.3.1 Local analysis of grid scale

The analysis begins by asking whether the scale of the grid pattern varies locally across an environment. For each 3-clique, the area is computed using Heron’s formula:

$$s_c = \alpha_c + \beta_c + \gamma_c$$

$$A_c = \sqrt{s \cdot (s - \alpha_c) \cdot (s - \beta_c) \cdot (s - \gamma_c)}$$

where $\alpha_c$, $\beta_c$ and $\gamma_c$ are the length of the three edges comprising clique $C_c$. This allowed the generation of ‘clique maps’ illustrating the local variation across the environment. Area was computed as a proxy for grid scale.

Having calculated the areas of the cliques, each area was divided by the maximal area across the environment, producing a dimensionless relative area $A_R = A_c / A_{\text{max}}$. For each environment, the relative areas were binned into a 10x10 grid and averaged. Contour plots were constructed from the resulting bins.

Fig. 6.2A shows the results of the local scale analysis. In contrast to the uniform shearing hypothesis, which is an affine (area preserving) transformation, the analysis shows significant variation in scale across the environment. Local scale was notably larger in the centre of the environment, but the $A_{\text{max}} / A_{\text{min}}$ ratio did not vary with the size of the environment (Fig. 6.2B).

Whether the observed effect is a central expansion or a boundary mediated contraction is unclear. However, the effect apparent from the pooled analysis presented in
Fig. 6.2A does not apply uniformly across all cells. In contrast, many cells showed a local contraction with proximity to one or more but not all edges (Fig. 6.2G, red bounded box). However, overall the scale appeared to be largest near the centre of the environment.

The scale ratio appeared to be related to the mean grid scale (defined as the mean length of all edges in the mesh; Fig. 6.2F). GCs with larger scales showed less scale variation across the environment whereas the opposite was true for smaller scales. A possible caveat to this finding is that GCs with the largest scales tended to have fewer fields. In these cases, the extrapolation of the cliques outside the boundary were more likely to match the properties of the observable fields, which by definition means less variation. However, this only applied to very large scales, whereas the effect seems to apply across the continuum.

### 6.3.2 Correspondence with firing rates

Chapter 4 proposed a model of grid pattern distortion based on biases in sensory input as provided by a set of PCs. Although the dataset did not contain simultaneously recorded PCs, a non-uniform distribution in density or firing rates of PCs might also produce a concomitant non-uniformity in the GC firing rates, assuming PC to GC projections. The same local analysis was therefore performed on the firing rates of each field.

The firing field was defined as the Voronoi region around each field centre (i.e. all points which are closer to field $i$ than to all other fields). For each field’s domain, the peak firing rate was calculated. The analysis showed a weak but similar effect to the local scale variation (Fig. 6.2C) where firing rates were greater in the centre of the environment. A similar visualization of the average firing rate maps (Fig. 6.2E) masked the effect.

The weak spatial effect was corroborated by a weak correlation between the peak firing rates and the local scale (area) across all cells (Fig. 6.2D).

### 6.3.3 Local analysis of grid rotation and distortion

The next analysis considered the local rotation of each clique. Each edge was first separated into three groups based on their orientation in an ‘ideal’ mesh (i.e. 3 groups with angles at $60^\circ$ apart; Fig. 6.1E). These groups defined ‘contour’ lines through the mesh which would remain parallel in an undistorted grid pattern. Relative orientation was defined for three groups as the orientation of each edge relative to the corresponding edge of the clique nearest the centre of the environment (Fig. 6.1E). The overall relative orientation $\theta_R$ was taken as the circular mean of the three orientations for each clique.

The analysis again indicated location specific orientation (Fig. 6.3A). Relative to
the central orientation, the absolute magnitude of the relative rotation increased
towards the boundaries of the environment.

Lastly, a distortion metric was defined to measure the ‘nonuniformity’ of the cliques
by taking the logarithm of the ratio between the longest and shortest edges:

\[ \Delta_c = \log \left[ \frac{\max(|E_c(i)| : i = 1 : 3)}{\min(|E_c(i)| : i = 1 : 3)} \right] \]

where \(| \cdot |\) denotes the Euclidean length of an edge. This definition is analogous
to the ellipticity measure defined earlier in this thesis when applied to a hexagon
constructed from the central 7 peaks of the autocorrelogram, which takes the ratio
of the semi-major and semi-minor axes of a corresponding ellipse. A value of 0
indicates an equilateral triangle whereas \(\Delta > 1\) indicates increasing non-uniformity.

Local distortive effects were less pronounced than the orientation and scale effects,
but nonetheless showed greater distortion away from the centre of the environment
(Fig. 6.3B). Interestingly, results from the largest 2.2m² environment suggest that
distortion was concentrated near the corners.

6.3.4 Local analysis of grid distortion and displacement

The analyses presented thus far give point properties of the distorted mesh, but
do not necessarily provide insight into the distortive mechanism. To address this
question a displacement metric was devised to analyse the movement of the fields,
assuming a hypothetical ‘ideal’ mesh.

Starting from the observed mesh, the ‘ideal’ mesh \(X^0\) was obtained by performing an
elastic relaxation, minimizing the total elastic energy in the mesh by translating the
nodes \(X\) so as to satisfy a global preferred edge length \(D_0\) (Fig. 6.3D, middle). \(D_0\)
was defined as the mean length of the edges of the central clique. The process can
be viewed as the inverse of the process described earlier which involved deforming
a uniform mesh to fit the observed firing pattern. Following the elastic relaxation,
the resulting mesh \(X^0\) was oriented and translated such that the central clique of
the observed and ideal meshes were maximally aligned (perfect alignment was not
possible if there was distortion in the observed mesh).

Given the two meshes, it was possible to define the displacement of each field, as
might be driven by a putative distortion process (Fig. 6.3D, right), by the relative
positions of each field \(X^0_i - X_i\).

As in previous analyses, the average displacement of the ideal fields were binned
([10x10 grid) and averaged. For each bin, a weighted polar histogram was con-
structed by multiplying each angular count by its corresponding magnitude (dis-
placement angles were binned according to \(\theta = 0 : 20 : 360^\circ\)).
The analysis (Fig. 6.3C) again corroborates earlier findings, indicating that fields near the edges and corners of the environment underwent the largest displacements. It was unclear from the analysis in what direction the average displacements were oriented. It is possible that the consistent directions were present in specific cells, but any such pattern were masked by the pooled analysis.

6.4 Discussion

Taken together, these results suggest that the distortions cannot be explained by a simple uniform shearing process since there is clear evidence that distortions are non-local. The most prominent of these distortions were a local contraction in scale approaching the environmental boundaries and an orientation misalignment with the centre-most grid pattern. To a lesser extent, local distortions were also increased near to the corners of the environment, an effect which was especially pronounced in larger environments.

An analysis of field displacement broadly corroborated these findings, suggesting that fields were displaced with a magnitude related to their proximity to environmental boundaries.

Stensola et al. (2015) showed that orientation offsets and accompanying ellipticity could be corrected by applying a local shear transformation. Whereas this transformation could in theory correct for rotation and distortion effects, the correction would apply globally such that locally uniform grid patterns would be distorted in the process. Moreover, a shearing process cannot explain local changes in scale.

The local variation in scale resembles a ‘barrel distortion’ (6.4A), whereby points are translated radially away from a central locus with a magnitude proportional to some exponent of their radius:

\[
X_d = X_c + (X_d - X_c) \cdot \sum_{k=1}^{N_K} K(k) \cdot R^k
\]  

(6.8)

where \(X_d\) and \(X_u\) are the distorted and undistorted points, respectively, \(X_c\) is the locus of the distortion and \(R\) is the distance of the undistorted point from that locus. \(K\) is a vector of distortion parameters describing the effect of radial distances of increasing order. Eq. 6.8 is more commonly known as a ‘barrel’ distortion. The parameters \(K\) can be modified so as to produce either local scale expansions (sources; Fig. 6.4A) or contractions (Fig. 6.4B).

A single barrel distortion does not produce tangential (relative to the centre of the environment) displacement as was evident from Fig. 6.3C, but can account for radial movement and local scale changes. By applying multiple barrel distortions, it
is possible to account for both the local scale changes and tangential displacement. When two barrel distortions are applied in opposite corners, the effect resembles a shearing transformation (Fig. 6.4B), with the addition of local scale changes.

To conclude, the analysis presented in this chapter suggests that grid patterns undergo a variety of different distortions (Fig. 6.4) which may affect local scale, orientation, distortion and displacement. Rather than a single distortive process, it is proposed that the vast majority of distortions can be explained by a single or combination of local scale expansions or contractions.

These local scale changes can be described mechanistically by the model proposed in chapter 4, the theoretical prediction being that the distortions should correlate with increased saliency, manifested by either biased associations to place cells with fields in those locations, or increased firing rates.

It is also possible that these distortions may be related to the learning rule implemented in the CA3 recurrent weights. In Chapter 5, it was shown that the true Euclidean distance could be recovered from the learned weights, given some assumptions about the form of the place field’s receptive fields, i.e. that they were Gaussian and of uniform variance across the environment. Of course, this is not observed experimentally; generally, there is diversity in the tuning widths and the receptive fields cannot always be described as Gaussian.

It remains to be explored whether learning the underlying structure of the environment based on realistic receptive fields might re-produce these local distortions, since any learned structure will dictate the grid pattern by virtue of the place-to-grid cell drive. In light of the thesis as a whole, and indeed the SLAM problem, the distortions explained in the online model (Chapter 4) and those that would be produced by the latter putative mechanism could be distinguished as ‘localization’ and ‘mapping’ based distortions, respectively.
Fig. 6.1
Fig. 6.1: **A** Local ellipticity in large boxes ([Stensola et al. (2015)](#)) **B** Theoretical predictions of non-uniform but periodic grid firing from [Dordek et al. (2015a)](#) (Top) and [Stachenfeld et al. (2017)](#) (Bottom) **C** Illustration of local smoothness constraint **D** Illustration of local scale constraint **E** Parallel lines used in the relative rotation metric. The rotation of each clique is defined by three angles, relative to the corresponding three angles of the central clique. The overall rotation is taken as the mean rotation relative to the angles of the central clique. **F** Example ‘clique maps’ showing local scale variation. **G** Example fits. Red bounded box shows example where the model-based fitting method allows the detection of fields with zero firing rates (‘missing’ fields)

Fig. 6.2: Contour plots constructed from the mean of data in a 10x10 bin grid. **A** Mean clique area as a proportion of the maximal clique area as a function of location in the three different sized environments. Minimum and maximum ratios are displayed above each plot. Grid scale is expanded in the centre of the environment (or equivalently, contracted near the boundaries). **B** Scale changes are the same across different sized environments. **C** Mean of peak field firing rates. Peak firing rates were also larger towards the centre of the environment, but the effect was weaker. **D** No strong correlation between firing rate and local scale. **E** Analysis of average firing rate maps hides the effect shown in **C**. **F** Area variation was greater for smaller grid scales.
Fig. 6.3: A Mean absolute rotation as a function of location, relative to the orientation of the central clique (see Fig. 6.1E). The grid pattern is also locally rotated away from the centre. B Distortion is concentrated near the corners of the environment. C Local displacement analysis corroborates with local rotation, distortion and scale effects. Each polar histogram shows displacement vectors for the corresponding spatial bin. Mean displacement magnitude indicated by size and colour. D Example of displacement analysis for a single cell. (Left) Mesh fit. (Middle) Ideal (red) and fitted (black) grid. (Right) Field displacement relative to the 'ideal' mesh, centred at the peak nearest the centre of the environment.
Fig. 6.4: Model distortions and examples from the experimental dataset (Stensola et al. (2015)). A Central ‘source’ causes local expansion in the centre of the environment. B Two ‘sinks’ (inverse sources) in the corners produces an effect that resembles a shearing process, but also captures local changes in scale. C A pure shearing process.
7. DISCUSSION

The important thing in science is not so much to obtain new facts as to discover new ways of thinking about them.

William Lawrence Bragg

Modern neuroscience is an exciting time for theorists and experimentalists alike. Thanks to new experimental techniques and a broader participation in science, it would be fairly trivial to state that we know more about the brain than we have ever before, if knowledge is measured in bits and bytes. However, it can feel (especially to the theorists) that we still barely understand anything at all. Early hypotheses about the brain - “region X does Y” - were in many respects conceptually straightforward, even if there was considerable implementational devil left to the detail. In this regard, a good hypothesis could be considered to be one that not only explains existing knowledge about the world, but also makes interesting and testable predictions. This modular view is of course still broadly true, however in modern neuroscience it is becoming increasingly clear that these boundaries are fuzzy, at best. Even superficial regions and their constituent cells can rarely be shown to perform one specialised function, such as responding to the colour blue or a specific ‘location in space’; instead they are often described more accurately by their responses to multiple factors. Moreover, rarely is processing truly feedforward; reciprocal connections are abundant in sensory cortices as they are in regions more traditionally considered to be ‘densely recurrent’ such that perception is influenced by prior beliefs in a reciprocal manner).

Much of this change in perception is being driven by the study of the hippocampus and its interaction with other regions. Place and grid cells have long been suspected to be associated with space, but new evidence is emerging to suggest that they might play a more generalized role in reward processing or navigation within conceptual spaces (Constantinescu et al. (2016); Garvert et al. (2017); Aronov et al. (2017)). The hippocampal field is in the envious position of having several good models of both the functional role and mechanistic operation of its constituent parts, which are becoming increasingly different to differentiate in terms of their experimental predictions. At the time of their discovery, the origin of the hexagonal firing pattern of GCs was mystery. Thirteen years later, there are now a multitude of detailed
models showing the various advantageous properties of the canonical grid pattern. Although many of these models have given us valuable insight, it is clear that in order to continue to advance our understanding, we must begin to analyze in detail those cases where neuronal behaviour deviates from normality. It was this principle that guided the investigation in this thesis, which attempted to gain insight from those departures from the 'canonical' grid firing pattern. This chapter is an attempt to not only recount its findings, but to summarize more holistically the perspectives that I believe that it might offer.

### 7.1 Results and predictions

#### 7.1.1 Chapter 2 - A functional analysis of GC firing pattern distortions

Chapter 2 began by investigating whether the experimentally observed grid pattern alignment offset to the walls of a square environment might arise through Hebbian-like interactions between GCs and BVCs or PCs, which were assumed to convey sensory information about the environment. Moreover, I hypothesized that if GC firing patterns were aligned through their interaction with environmental boundaries, these differences should be evident by studying their alignment with respect to their environment and grid properties.

An initial analysis suggested that specific relative orientations might minimize the variance in firing rate correlation of each GCs firing pattern across a given module with its sensory input, and that this orientation might relate to the ratio of the grid scale and its enclosing environment. Analysis of experimentally observed cells in square boxes showed that such a relationship might be present in the data, although the analysis was inconclusive, due in part to the relative absence of data from GCs with small scales in large environments.

Further analysis of this theoretical result suggested that it was unlikely to be true for non-ideal grid patterns. Moreover, it was suggested that the orientation offset was accompanied and might be driven by a concomitant shear transformation that might also develop with experience. Testing this hypothesis, further simulations showed that, by allowing GCs to perform a Hebbian-like gradient descent to minimize overlap variance by modifying the geometric properties of their firing patterns, the result was an orientation that oscillated with intrinsic scale about a mean of $7.5^\circ$, accompanied by a shearing distortion.

#### 7.1.2 Chapter 3 - reproducing distortions in a CAN model of GC firing

Although the results from the previous chapter were encouraging, they were based purely on geometrical analyses and did not offer any insight into the mechanistic

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1 The dataset from chapter 6 did not become available until recently. Further work will extend the analysis from chapter 2 to include it.
generation of the alignment and accompanying shearing distortions. A particular weakness of these analyses was that there was nor principled way of imposing a penalty on deviations from uniform hexagonality. Chapter 3 attempted to bridge this gap by considering the CAN model of grid cell firing. CAN models are a natural candidate for the analysis as they constitute a population level description of GC firing.

Firstly, the attractor dynamics that lead to the establishment of the hexagonal grid pattern are shown to have an intrinsic resistance to deformations. Nonetheless, initial simulations showed that it was possible to stably deform a static multi-bump attractor pattern by applying strong stimulation to the attractor sheet, as might be provided by strong sensory inputs, in combination with an experience-dependent rescaling (Barry et al. (2012)). Moreover, under a specific pattern of stimulation, the attractor pattern tended to deform so as to resemble a shearing transformation. However, it was concluded that such a pattern (simultaneous activity at locations corresponding to opposite corners of a square box) was unlikely to arise biologically. Stimulation by sensory associations learned in a Hebbian manner did not reproduce the same results, since the resulting stimulation pattern did not represent a close enough energetic optimum to be able to distort the attractor pattern without completely overriding it. Furthermore, it was unclear how the results might translate to a distortion in the readout pattern, which is generated by plotting the activity of a single cell against the location of the animal in space, where the attractor pattern is translated to follow this movement.

We next hypothesized that distortions in the readout may not be the result of the translation of a deformed base pattern, but might instead arise as a temporal average of the translation of an undistorted pattern. However, it was found that a contraction of the grid scale with both fixed and continuously modified pre-learned associations either disrupted the grid pattern (strong stimulation) or produced a smearing effect which was best described by two superimposed but spatially offset patterns.

We proposed that this failure was a limitation of the model of sensory input to the GCs. CANs are defined by their winner take all dynamics, such that corrective sensory input will tend to either dominate the current activity pattern or be ignored. It was argued that such a mechanism was not suitable for producing continuous distortions to the grid pattern.

7.1.3 Chapter 4 - Probabilistic integration in GCs

Our analyses in chapter 4 revealed another weakness of current attractor models, which was that their intrinsic dynamics complicate the task of learning in novel environments under perceptual ambiguity. The main concern of chapter 4 was therefore
to devise a more principled method of updating the grid pattern with sensory input, with the principal aim of developing a system that could not only learn in novel environments, but also reproduce the characteristic distortions analyzed in previous chapters.

Firstly, a novel theory of GC firing was developed based on the principles of Bayesian integration and recursive filtering, implementing a ‘soft-resetting’ mechanism that was dependent on the perceived noise in each of the sensory and PI signals. Unlike previous CAN and SLAM models of GCs, this model does not rely on attractor dynamics (Milford et al. (2010)) or particle re-sampling (Cheung (2016)). Nonetheless, it was observed that the firing of GCs in a module maintained their spatial relationships in a ‘modular’ fashion. Instead, the proposed model relies on a similar twisted-torus connectivity (Guanella et al. (2007b)) but can support arbitrary distributions.

The model responded parametrically to environmental manipulations (Barry et al. (2007); Stensola et al. (2012)), which was interpreted as a dominance of sensory over PI information. The model also suggests that deformations in non-rectangular environments (Krupic et al. (2015)) could be caused by prior beliefs reflecting previous experience.

These prior beliefs are assumed to be effected through the synaptic associations between PCs and GCs. When PCs fire, they drive the activity of the grid population towards their associated GCs. Extending this idea, I showed that non-uniformities in the distribution of the firing rates or locational densities of the sensory PCs can over-represent physical locations in grid space. These non-uniformities had the effect of warping the perception of space, manifesting in a sheared grid pattern under specific conditions. However, other distortions could be produced by varying the form of the distribution describing the firing rates or densities of the PCs. Although it was not shown, it is possible that the same effect might arise from non-uniformities in the PC-GC associations, resulting from biased trajectories causing faster learning in some regions of the environment.

Lastly, I demonstrated that GCs can be used to disambiguate otherwise perceptually similar environments, driving re-allocation of sensory-GC associations. I further proposed that such a mechanism might produce PC remapping, suggesting that the PC-GC interaction is bi-directional.

The proposed model makes several experimentally testable predictions. The first and most apparent is that the tuning width of the grid fields should vary both with locational uncertainty an with experience. If such an effect were present in GCs...

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2 Experimental animal trajectories are often biased towards the corners and edges of an environment, especially with experience.
firing, it has not (to the authors knowledge) yet been tested. However, the effect might also be difficult to detect over the limited navigational ranges (<3m) studied in most laboratory setups.

7.1.4 Chapter 5 - Offline learning an inference in GCs

Although the system developed in the previous chapter was capable of converging on a stable solution to the SLAM problem under certain conditions, this ability was hampered in more complex environments and/or higher navigational/perceptual ambiguity. Chapter 5 was therefore concerned with a more principled analysis of the crucial computational requirements of performing SLAM.

Based on theoretical and practical insights from the SLAM literature, I argued that an ideal navigational system would need to make be able to perform inference on observations of its environment. Accordingly, I proposed that PCs in CA3 might not only represent a metric map of the environment, but might also be used to perform offline inference by exchanging information.

Firstly, an algorithmic solution was proposed, demonstrating that such an inference process could be achieved via a message passing process. Agents imbued with this ability were capable of both faster and more powerful reasoning about the structure of their environments. Inference was demonstrated to be more effective and less energetically costly when a principled scheduling scheme was implemented. The update schedule of the PC graph is determined by the relative confidence of local regions about their current beliefs.

The PC reactivations produced by this scheduling process bore a resemblance to the phenomenon of hippocampal replay, suggesting that it may be interpreted as a process of propagating information through a graph representing the structure of the animal’s environment. Unlike most existing models of SLAM in the robotics literature, I proposed that the online system is in most cases sufficient for navigation in simple environments. However, when predictions from the online system disagree with incoming sensory information, the ‘prediction error’ may trigger the engagement of the offline system. Such a process may be manifested in the the hippocampus as sharp-wave ripples and associated replay events.

Chapter 5 was concluded by developing a neurally plausible model capable of implementing belief propagation. The proposed mechanism is based on propagation of information by neural travelling waves, which trigger synaptic changes by eliciting synchronised spiking in the PC an GC populations.

7.1.5 Chapter 6 - Novel insights from GC analysis

I concluded this thesis by offering a more detailed analysis of the grid pattern. By developing a novel analysis technique, I confirmed that grid patterns are indeed less
‘canonical’ than is often considered. Moreover, it is argued that while the ‘uniform shearing’ hypothesis proposed by Stensola et al. (2015) may be useful in some cases as a broad description, it does not fully account for the observed distortions to the grid pattern.

Unlike in uniform shearing transformations, there were significant local variations in the scale, orientation and non-uniformity of the grid pattern. The relative grid scale was consistently smaller at the edges of the environment. Relative to the central orientation of the grid pattern, rotation was also systematically misaligned at the edges. Non-uniformities were concentrated in the corners. These local deformations were to a lesser extent reflected by decreased firing rates near the edges.

Taken together, our analysis suggests that distortions to the grid pattern can be better understood by local barrel distortions. Multiple barrel distortions applied to opposite corners of the environment can reproduce not only the local scale changes but also the local rotations observed. Our analysis broadly corroborates the model proposed in Chapter 4, although more work is to be done to show this conclusively.

7.2 Outlook

Is is my opinion that the work presented in this thesis should be viewed less as a collection of results and more as a useful perspective. Perception of the function of the hippocampus has developed significantly over the better part of the past century since Tolman’s conception of the cognitive map in 1948, insight into memory through patient H.M. and the discovery of place cells in 1971. In 2005, the discovery of grid cells influenced further development in theories of the function of the hippocampal formation.

Two significant directions of research have influenced recent work, the first being the demonstration that both place and grid cells encode position in non-physical (conceptual) space and secondly, the possible influence of reward on their firing. In this section, I argue that these interpretations are complementary to the more traditional spatial interpretation. Moreover, whereas in this thesis we have only considered the navigation of physical space, the theory extends naturally to conceptual spaces.

7.3 What can neuroscience learn from SLAM?

7.3.1 Holistic approaches to SLAM

SLAM provides a rich framework within which to understand spatial processing in the brain. Although the circuitry is different, some functional aspects must be shared, since both brains and machines are tasked with operating in the same complex environments.
Despite these commonalities, theories of navigation in robotics and neuroscience have largely evolved independently. Where neuroscientific theories were developed to respect the constraints of biology, research in robotics has developed rich theory describing how spatial perception and learning can be ideally and practically implemented. The latter is important; rarely are biological models tested as rigorously in environments as demanding as the real world, but more thorough testing of this kind might yield new insights into the true requirements of cognitive tasks.

Bayesian statistics also constitute a natural framework for dealing with perceptual ambiguity and multi-modal information (see Chapter 4). Whereas it cannot be expected that the brain operates in a homogeneously and perfectly Bayesian fashion (other factors contribute to the cost function), the theoretical guidelines nonetheless remain useful. Developing hypotheses within a Bayesian framework could be considered the first level in the context of Marr’s computational hierarchy, but fortunately it is often possible to draw on a rich body of existing work to help to develop these models along the algorithmic and computational levels, so as to be more reconcilable with neurophysiology (Pouget et al. (2013)).

An important emerging message from SLAM research is the holistic treatment of the processing hierarchy. Early approaches to SLAM were mostly modular in nature, with each stage of the processing hierarchy tailored to a specific function and often requiring significant manual engineering. Modern SLAM systems increasingly treat the processing and inference hierarchy as a single optimization problem (Cadena et al. (2016)). Visual perception is used for localization, but a belief over current location can also be used to influence perception. This reciprocal influence has recently been shown to be utilized in the brain; neurons in V1 were demonstrated to respond more to a landmark in one location that to a visually identical landmark in another location. Moreover, the errors in subjective localisation calculated by comparing neuronal response from V1 and CA1 were correlated, suggesting that the response of V1 neurons is influenced by subjective spatial position (Saleem et al. (2017)). The HPC may also be involved in actively directing visual search (Nau et al. (2018); Julian et al. (2018)).

Another key development in SLAM was to realize the importance of sparsity. In the context of graph-based methods, this sparsity is dictated by the complexity of the underlying factor graph; if all measurements are considered the inference process grows quickly in complexity, quickly becoming intractable and/or impractical. Sparsification methods (Ila et al. (2010)) reduce this complexity by pruning less informative measurements (nodes) and their associated factors (influences on other nodes). These methods have also been found to be effective in reducing the computational requirements of large DNNs without compromising on performance (Aghasi et al. (2016)). Sparse representations have been found across several brain regions.
including (but not limited to) primary visual, olfactory, auditory and somatosensory cortices, among others (see Olshausen and Field (2004) for a review). Sparsity has long been known to be important to Hippocampal processing, where only 40% and 30% of neurons in CA1 and CA3 respectively are active anywhere in a given environment. One study found that this proportion is variables in time; CA1 neurons were twice as likely to fire in novelty as with experience of an environment, ‘pruning’ the activity of cells with low firing rates over time (Karlsson and Frank (2008)). Thus, sparsification is likely to be an active process in the brain, rather than simply a physical limitation in connectivity.

7.3.2 Useful representations of space

It is often assumed that the ‘cognitive map’ represented by PCs is metric in nature. Given dense enough coverage, the exact geometrical features of space can be decoded accurately by considering the overlap - or correlations - of each PC node. Such a representation might correspond to a ‘point-cloud’ of dense features (but only up to the diameter of the largest place field).

SLAM research as traditionally employed two forms of map representation. Metric maps (Fig. 7.1B, left) represent environments as discretized grids, where each ‘pixel’ might represent the probability of occupancy of an object. On the other hand, topological approaches represent an environment using graphs of interconnected landmarks such as doorways, connected by edges if they can be traversed without passing through another landmark (Fig. 7.1B, right).

Both approaches have their strengths and weaknesses. Metric maps are comparatively easy to compute and maintain in large scale environments (Burgard et al. (1996)). They also aid in the recognition of landmarks by encoding their relative geometrical relationships, independent of view-point and permit the computation of shortcuts (Thrun (1998)).

In contrast, topological maps cannot aid in object recognition since they only encode statistical contingencies between observations. The determination of salient ‘landmarks’ or ‘critical points’ (Fig. 7.1B, middle) is a difficult computational challenge in itself. However, once encoded topological representations are far more data efficient; their ‘resolution’ is only related to the complexity of the environment (i.e. a featureless corridor with a start and end has a very simple topology). Navigation using topological maps does not rely explicitly on an exact geometric estimate of location, so can in practice often recover better from errors than grid-based approaches (Thrun (1998)). Topological representations are also more amenable to planning, since they naturally represent discrete ‘objectives’.

3 The model proposed in chapters 4&5 is an example of a grid-based or metric mapping approach.
Fig. 7.1: A System diagram of a possible hippocampal circuit for determining and navigating within task-relevant subspaces $T(s)$ of the total sensory input space $S(t)$. A multidimensional reward signal $R(t)$ may be necessary for determining the relevant task-spaces. B Metric vs. topological representations of space (Thrun (1998)). C A SLAM system encoding a hierarchical representation of space (Grisetti et al. (2010b)).

Recognizing this distinction and constructing models that build topological representations might help to better interpret neural responses. In the case of PCs, developing a topological model of spatial representation might make useful predictions about the spatial density of place fields (Hollup et al. (2001)).

Several SLAM approaches in fact make use of join metric-topological representations to allow the best of both worlds (Thrun (1998); Konolige et al. (2011)). But how could this relate to the HPC? An interesting proposal would be to assume a dual function for BVCs, which are most often considered to drive PC responses. Whereas the latter function could still be true, PCs encoding topological representations might plausibly drive BVCs in a ‘bottom-up’ manner to facilitate geometric interactions with the local environment by predicting proprioceptive information (local metric maps), or to reconstruct viewpoint-dependent egocentric representation to support recollection from memory (Bicanski and Burgess (2018)).

7.3.3 Cognitive maps for abstract inference

Navigating conceptual space

In the context of cognitive representation, the ‘physical’ space considered throughout this thesis is only one instance of ‘space’ in the the more general sense. Nevertheless, physical space appears to be an especially important subspace to the HPC, given what is known about the tuning properties of PCs and GCs. However, given recent findings that GCs and PCs can also represent conceptual spaces (Constantinescu et al. (2016); Aronov et al. (2017)), an important direction of current and future research is in determining the extent of this common representation. It is highly unlikely that the hexagonal firing response of GCs would have been discovered if they
only encoded non-spatial variables since revealing this structure requires correlation against variation in that variable. However, the discovery of GCs have since led to the discovery of ‘grid-like’ responses in the visual cortex of nonhuman primates (Killian and Buffalo (2018)) and humans (Nau et al. (2018); Julian et al. (2018)), suggesting that periodic encoding strategies may be a general computational principle.

A second important question is whether the over-representation of space in the HPC reflects task demands or an evolutionary bias. The presence of other navigationally relevant cells (BVCs, HDCs) in surrounding areas suggests the latter, however there is likely to be some plasticity in the responses. A small proportion of GCs that responded to ‘location’ in an auditory task also produced hexagonal firing response when the animal was allowed to navigate in a spatial environment (Aronov et al. (2017)).

Determining relevant sub-spaces

Ultimately, time underpins all computations in the brain, since biological processes evolve at physically determined rates. In order to navigate through any type of space there must be some estimate of velocity, such that total ‘distance’ can be integrated against biological time. Thus, PI is still a relevant functional hypothesis for GCs, but in the sense of integrating the rate of change of some abstract stimulus.

The function of the GC system could therefore be described as follows. GCs receives a set of time varying stimuli defined as the vector $\mathbf{S}(t) \in \mathbb{R}^N$, where $N$ is the dimensionality of the stimulus space. The function of the system is firstly to determine the subspaces of $\mathbf{S}$, which we denote $\mathbf{T}(t) \in \mathbb{R}^{N_T}$, that are most relevant to some task or cost function. This is equivalent to finding the function:

$$f : \mathbf{S} \rightarrow \mathbf{T} \quad (7.1)$$

which maps the stimulus to the the task-spaces. Once this mapping function $f$ has been found, the next function of the system is to use this mapping to navigate within the identified task-spaces. From here, the same SLAM framework applies; estimates of location may be determined jointly from sensory estimates corresponding to known task states and by integrating task-space velocity over time.

But what are these task-spaces and how could they be discovered to allow GCs to encode relevant representations? Ultimately, this is a question of the function of the GC system and its inputs, but consider a few possibilities:

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4 BVCs and HDCs might also plausibly represent proximity to and direction within some abstract task space.

5 Velocity might also be measured as the rate of change with respect to another stimulus dimension, but ultimately time is the only independent variable.
Dimensionality Reduction  Optimizing for reconstruction error is the basis of common dimensionality reduction techniques (e.g. PCA, ICA, IsoMap). Such a technique produces grid-like responses when performed on the firing fields of PCs encoding location or transitions between states \( \text{[Dordek et al. (2015a); Stachenfeld et al. (2017)]} \).

Slow-feature Analysis  Wiskott et al. (2003a) posed the problem of discovering relevant task spaces as finding a set of input-output function \( g : \mathbf{x} \rightarrow \mathbf{y} \) such as to minimise the rate of change of \( \mathbf{y} \), on the basis that ‘useful’ information changes slowly and continuously over time.

Reward-based encoding  If task-spaces are to be directly related to task-performance, the function \( f \) might take as input some time-varying reward signal \( \mathbf{R} \). The reward signal itself is of course just another feature of the stimulus space, but it may have special significance as a supervised learning signal in the brain in the form of dopamine \( \text{[Schultz et al. (1997)]} \).

7.3.4 What can SLAM learn from neuroscience?

Behaviourally guided localisation and mapping

There has been much recent interest in GCs as a useful representation for performing model based reinforcement learning \( \text{[Stachenfeld et al. (2017)]} \). As discussed in the introduction to this thesis, this hypothesis assumes that GCs represent a low-dimensional encoding of the successor representation \( M(s', s) \), which represents the discounted expected number of transitions to state \( s' \) given current state \( s \) \( \text{[Dayan (1993)]} \). \( M \) is assumed to be encoded by PCs, which would be expected to have directionally skewed firing fields in environments where animals take stereotyped trajectories such as linear tracks \( \text{[Mehta et al. (2002)]} \). However, despite the fact that grid-like responses can theoretically result from performing dimensionality reduction on the successor representation, it is also true that similar methods applied to a population of PCs with Gaussian receptive fields produces similar results \( \text{[Dordek et al. (2015a)]} \). Under a random walk policy, the firing fields of successor-PCs would of course resemble Gaussian receptive fields; the important point here is that the SR of GCs is not inherently tied to actions.

However, it is clear that encoding the transition structure is in general a useful representation. As discussed in chapter 1, GCs have been implicated in PI, location decoding, vector navigation and relational knowledge, low dimensional encoding of PC population firing and model-based planning. It is possible that GCs contribute in part to all these functions, however the sheer breadth of theoretically interesting properties that GCs putatively possess suggests that their form might be useful in guiding the development of other cognitive systems.

To link the work in this thesis to the RL interpretation, it should of course be
pointed out that in most behavioural domains such as navigation, there is inherent uncertainty associated with state transitions. Traditional RL based on MDPs can in fact deal naturally with uncertain state transitions following an intended action, but rely on being able to observe the true result. In contrast, SLAM deals with the problem of not knowing the result of certain transitions. When state uncertainty is introduced to RL problems, the result is a partially observed Markov decision process (POMDP). Whereas RL learns and evaluates action policies over states, POMDPS consider belief states, which are themselves probabilistic in nature. We will not discuss POMDPs any further other than to emphasize that SLAM and RL are not incompatible, but both incomplete parts of one unifying theory.

For both RL and SLAM research, this is an important link. SLAM has traditionally been concerned with generating maps of an environment independent of their intended use; i.e. “given sensor data $z_{0:k}$ and perceived trajectory $x_{0:k}$, figure out the map and the location within it”. In contrast, active SLAM (Feder (1999); Leung et al. (2006)) considers the problem of optimally navigating so as to reduce the uncertainty of one’s map representation. However, even this definition imposes a constraint on the behaviour of the system, namely that the aim is still first and foremost to perform mapping. Real-world applications might yet benefit from more research into truly task-guided SLAM. In this scenario, there would be clear benefits to learning the transition structure of an environment rather than assuming the form of a noise model (as was assumed in this work).

**Grid cells as hierarchical representations**

If GCs are truly beneficial for navigation and mapping, their hierarchical structure is surely a crucial component. Traditional approaches to SLAM have considered the optimization of a single map (or combinations of metric-topological maps), there has been some work in the area of submapping (Estrada et al. (2005); Grisetti et al. (2010b)) which divides the factor graph into a series of smaller subgraphs. Each subgraph is independently optimized (often in parallel) before global alignment and refinement.

The subgraphs may simply be equal divisions of the same resolution, however one approach proposes a true hierarchical solution (Fig. 7.1C; Grisetti et al. (2010b)). In this scheme, observations initially cause refinement of a coarse representation whereby observations first affect a coarse representation. Optimization proceeds selectively down the hierarchy, only effecting changes to regions that were most affected by changes at the coarser levels. This method appears mainly to have been proposed as a solution for improving the SLAM performance on traditional

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6 Markov decision processes describe a systems in which each state has an associated action which leads (possibly stochastically) to the next state. States may have an associated reward. Each state-action pair is conditionally independent of previous states and actions.
benchmarks. However, there is much neuroscientific interest in the ability of such a hierarchical system to efficiently incorporate and reason with new information (Behrens et al. (2018)). In the SLAM context, a hierarchical representation of space would be naturally suited to encoding multiple non-local maps discovered independently, but were later connected by higher level structure.

7.4 Open questions and future work

7.4.1 Replay as a cognitive marker of information propagation

Perhaps the most interesting experimental prediction of this thesis (chapter 5) is that replay events reflect propagation of structural information through the PC graph. A significant change in the belief of PCs over their location (in GC space) would manifest as a change in the location of their firing fields following a replay event.

I propose the loop closure simulation in chapter 5 as a suitable experimental setup if conducted in VR. By changing the movement gain, the prediction error induced when the animal completes a single lap of the track can be controlled. Replay events would be expected to be more frequent when the gain is set to low values (such that the animal is surprised to have already completed a lap) than when the gain is set to unity.

7.4.2 Do place cells remap in conjunction with global GC realignment?

In chapter 4 we simulated an experiment whereby GC firing pattern were found to become globally consistent when two previously local representations were connected by metric information (Carpenter et al. (2015)). Although we did not explicitly model the remapping of PC firing rates, our simulations suggest that such a mechanism could drive re-association of the GC-PC weights.

It is unknown whether PCs remap in conjunction with this local realignment in such a context, although this has been shown to be true in more typical dim-sabiguation tasks (Fyhn et al. (2008)). As discussed in chapter 4, several studies (Skaggs and McNaughton (1998); Fuhs et al. (2005); Spiers et al. (2013)) recording PCs show that their responses are driven strongly by sensory information, mirroring their response across perceptually identical environments. However, the rate of realignment was shown to be slow in GC (several weeks), suggesting that PC responses might need to monitored (in parallel with GC responses) over longer time-scales (Lever et al. (2002b)).

7.4.3 PC driven distortion of the GC firing pattern

Our simulations (chapter 4) and analysis (chapter 6) together suggest that local distortions to the GC firing pattern might be driven by non-uniformities in either the PC density or firing rates of the PCs connected to the GCs. Indirect evidence
suggests that local scale changes, rotations and deformation are weakly correlated with GC firing rates, however direct evidence from simultaneously recorded GCs and PCs would be required to provide a more concrete answer.

### 7.4.4 Hierarchical information propagation

In current simulations, we consider GCs as a substrate in which to encode the location distributions of landmarks (PCs), however our work did not address a mechanism of encoding multiple maps over different GC modules. Theoretically, SLAM could occur independently over multiple modules, however the more intriguing question is whether such a representation is truly advantageous. Further work will extend our model of belief propagation to multiple scales to investigate this possibility.

**Reward or localization driven exploration?**

In the previous section our discussion touched on the relationship between active SLAM and reward-guided behaviour. An intriguing question is whether these theories can be compared in explaining typical animal trajectories. This could in principle be achieved by using a ‘meta-learning’ RL approach ([Wang et al. (2018)](Wang)) to train a simulated agent maximize either some function of exploration-exploitation ([Thrun (1995)](Thrun)) related to map-building, or the total expected cumulative reward to determine optimal trajectories in both regards.

**How flexible are GC representations?**

As discussed earlier, GCs have been shown to be able to encode state information in an auditory and spatial context ([Aronov et al. (2017)](Aronov)), but it remains unclear whether these representations are conjunctive or task-dependent. We propose the following experiment.

A mouse on a linear VR track is trained to walk forwards with no visual input until a reward location is reached. The gain in the animal’s movement is modulated over trials and indicated by a coloured visual stimulus. Accurate prediction of the reward location would require GCs to adopt a conjunctive color × self-motion representation.
APPENDIX
A. METHODS FOR GRID CELL ANALYSIS

A.1 Autocorrelogram

The autocorrelogram of the ratemap at a single position \([\tau_x, \tau_y]\) is the correlation of the raw ratemap and a spatially offset ratemap with offset equal to the position:

\[
 r(\tau_x, \tau_y) = \frac{n\Sigma \lambda_1(x, y)\lambda_2(x - \tau_x, y - \tau_y) - \Sigma \lambda_1(x, y)\Sigma \lambda_2(x - \tau_x, y - \tau_y)}{\sqrt{n\Sigma \lambda_1(x, y)^2(\Sigma \lambda_1(x, y))^2} \sqrt{n\Sigma \lambda_2(x - \tau_x, y - \tau_y)^2(\Sigma \lambda_2(x - \tau_x, y - \tau_y))^2}} \quad (A.1)
\]

A.2 Gridness score

The gridness score measures the rotational symmetry of the autocorrelogram at 30° intervals:

\[
 Gridness = \frac{1}{2}(G_{60} + G_{120}) - \frac{1}{3}(G_{30} + G_{90} + G_{150}) \quad (A.2)
\]

where \(G_i\) is the correlation between the autocorrelogram rotated at \(i°\) and the original autocorrelogram.

A.3 Calculating ellipticity

Ellipticity was determined from simulated and experimentally observed GC rate maps by first obtaining the semi-major and semi-minor axes. These were obtained by isolating the six inner-most firing fields of the autocorrelogram and using a least-squares method to fit an ellipse to their centroids. Any ellipse can be described by the general equation:

\[
 f(x, y) = ax^2 + bxy + cy^2 + dx + ey + f = 0 \quad (A.3)
\]

From which the semi-major and semi-minor axes can be determined from:

\[
 r_a = \sqrt{\frac{2(af^2 + cd^2 + gb^2 - 2bdf - acg)}{(b^2 - ac)(\sqrt{(a - c)^2 + 4b^2} - (a + c))}} \quad (A.4)
\]
The ellipticity and eccentricity scores can be calculated as functions of the ratio of the semi-minor and semi-major axes.
B. ANALYTICAL PROOF OF SHEARING BY NON-UNIFORM PC DENSITY

B.1 PC→GC weight structure

In the real simulation, the weights are learned via the BCM rule. The weights between the pre and post-synaptic cells (place and grid cells, respectively) change according to their average co-firing over a short time-period, modulated by a sliding threshold:

\[
\frac{dw_{pg}}{dt} = P_p(t)G_g(t)(P_p(t) - \theta(t)) \quad (B.1)
\]

\[
\frac{d\theta}{dt} = P_p(t)^2 - \theta(t) \quad (B.2)
\]

The steady-state weights in the case where the two cells do not influence each others’ firing (i.e. the firing of each is independent) approximate the covariance between the two firing patterns (see B.1 for a numerical illustration in 2D).

In 1D, this corresponds approximately to the integral (assuming an infinitely long track):

\[
W_{pg} = \int_{-\infty}^{\infty} P_p(x)G_g(x)dx \quad (B.3)
\]

The firing pattern of GC \(G_g(x)\) can be approximated as the sum of multiple Gaussians with means separated periodically across space:

\[
G_g(x) = \sum_{i=-\infty}^{\infty} \mathcal{N}(x, \mu_{ig}, \sigma_g) \quad (B.4)
\]

Where \(\mu_{ig} = i\phi_g\) and \(\sigma_g\) are the centre of mass and tuning width of the grid fields, respectively and \(\phi\) the grid scale. Place cells are also modeled as Gaussians:

\[
P_p(x) = \mathcal{N}(x, \mu_p, \sigma_p) \quad (B.5)
\]
Where $\mu_p$ is the preferred centre of firing of a given PC. The product of two Gaussians is also Gaussian such that:

$$W_{pg} = \int_{-\infty}^{\infty} \sum_{i=-\infty}^{\infty} S_{pg,i}(x, \mu_{pg,i}, \sigma_{pg}) dx \quad (B.6)$$

Where:

$$\mu_{pg,i} = \frac{\mu_p \sigma_g^2 + \mu_g \sigma_p^2}{\sigma_p^2 + \sigma_g^2} \quad (B.7)$$

$$\sigma_{pg} = \sqrt{\sigma_p^2 \sigma_g^2} \quad (B.8)$$

$$S_{pg,i} = \frac{1}{\sqrt{2\pi(\sigma_p^2 + \sigma_g^2)}} \exp \left[ -\frac{(\mu_p - \mu_{gi})^2}{2(\sigma_p^2 + \sigma_g^2)} \right] \quad (B.9)$$

The weight $W_{pg}$ is the evaluation of the integral in equation $B.6$:

$$W_{pg} = \sqrt{2\pi \sigma_{pg}^2} \sum_{i=-\infty}^{\infty} S_{pg,i} \quad (B.10)$$

Thus, the weights from a PC with centre of firing $\mu_p$ and tuning width $\sigma_p$ to a single GC $G_g(x)$ with corresponding mean and covariance are also described by a Gaussian function:

$$W_g(\mu_p, \sigma_p) = \sqrt{2\pi \sigma_{pg}^2} \sum_{i=-\infty}^{\infty} N(\mu_p, \mu_{gi}, \sigma_p^2 + \sigma_g^2) \quad (B.11)$$

**Fig. B.1**: Steady-state weight learned using the BCM rule approximate the covariance (overlap) between the firing of PC-GC pairs.

### B.2 Re-weighting the PC activity

Given the steady-state weights learned in the previous section, if they were then to drive GCs from the firing of a population of PCs distributed uniformly across all
space, the output firing of GC \( G_g(x) \) be given by:

\[
G_g(x) = \int_{-\infty}^{\infty} p(\mu_p, x) \cdot W_g(\mu_p, \sigma_g) \cdot R(\mu_p) d\mu_p \quad (B.12)
\]

Where \( R(\mu_p) \) is some re-weighting function which modulates each PC’s activity by its location in space and \( p(x, \mu_p) \) is the continuous version of eq. B.5 where place cells are assumed to be uniformly distributed throughout space for analytical simplicity.

The Gaussian PC and weight terms in the above can again be combined into a single Gaussian giving a simplified expression:

\[
G_g(x) = \int_{-\infty}^{\infty} R(\mu_p) \sum_{i=\infty}^{\infty} S_{c_i} \mathcal{N}_{c_i}(\mu_p, \mu_{c_i}(x), \sigma_c) \cdot d\mu_p \quad (B.13)
\]

Where:

\[
\mu_{c_i} = \frac{\mu_{g_i} \sigma_p^2 + x(\sigma_g^2 + \sigma_p^2)}{\sigma_p^2 + (\sigma_g^2 + \sigma_p^2)} \quad (B.14)
\]

\[
\sigma_c = \sqrt{\frac{\sigma_p^2(\sigma_g^2 + \sigma_p^2)}{\sigma_p^2 + (\sigma_g^2 + \sigma_p^2)}} \quad (B.15)
\]

\[
S_{c_i} = \sqrt{\frac{\sigma_{pg_i}^2}{\sigma_p^2 + (\sigma_g^2 + \sigma_p^2)}} \exp \left[ -\frac{(x - \mu_{g_i})^2}{2(\sigma_p^2 + (\sigma_g^2 + \sigma_p^2))} \right] \quad (B.16)
\]

The re-weighting function \( R(\mu_p) \) is now defined as a quadratic exponential:

\[
R(\mu_p) = \exp(\alpha + \beta \mu_p + \gamma \mu_p^2) \quad (B.17)
\]

Eq. B.13 can now be evaluated as:

\[
G'_g(x) = \frac{1}{2\pi(2 + 1/\sigma^2)} e^{-\frac{1}{2(1+2/\sigma^2)}(x + \beta \sigma^2 - \epsilon \mu_g)^2} \quad (B.18)
\]

where \( \epsilon = 1 - 2\gamma \sigma^2 \) and \( G'(x) \) is the reweighted GC firing pattern.

**B.2.1 Equivalence of reweighting and linear shift**

Differentiating B.18 wrt \( x \) and solving \( \frac{dG'_g}{dx} = 0 \):

\[
x_{\text{max}} = -\beta \sigma^2 + \epsilon \mu_g \quad (B.19)
\]
The peak locations in eq. [B.19] equate to the centres of the grid firing fields (each \( g \) corresponding to a single field), which are linearly shifted according to the parameters \( \beta, \epsilon, \sigma \) and \( \mu_g \). Thus, the exponential-polynomial reweighting function in eq. [B.17] defines a linear shift of the grid fields which is a function of their original location and their tuning width.

To demonstrate this result more directly, it is instructive to first define the base GC firing pattern \( G^0_g(x) \) by setting all coefficients in eq. [B.17] equal to zero. Applying a linear coordinate shift obtains:

\[
G^0_g(a + b \cdot x) = \frac{1}{\sqrt{6\pi\sigma^2}} \exp\left(-\frac{1}{6\sigma^2}(a + b \cdot x - \mu_g)^2\right)
\] (B.20)

Which is a linear shift of the base firing pattern. Comparing the coefficients of eqs. [B.20] and [B.18]

\[
a = \frac{1}{\epsilon(1 + 2\epsilon)}(\epsilon(1 + 2\epsilon)\mu_g \pm \sqrt{3\epsilon(1 + 2\epsilon)(-\beta\sigma^2 + \epsilon\mu_g)})
\] (B.21)

\[
b = \mp \frac{\sqrt{3}}{\epsilon(1 + 2\epsilon)}
\] (B.22)

which, since the solution exists shows that the whole grid firing pattern (as opposed to the peaks) is subject to the linear transformation. The results in eq. [B.19] can be recovered by setting \( x = \mu_g \).

Since it would be interesting to know how the grid pattern is shifted relative to the some focal point of shifting \( x_c \), the reweighting function can be re-cast as:

\[
R_c = e^{r_0 + r_1(\mu_p - x_c) + r_2(\mu_p - x_c)^2}
\] (B.23)

where \( \alpha = r_0 - r_1x_c + r_2x_c^2 \), \( \beta = r_1 - 2r_2x_c \) and \( \gamma = r_2 \). Thus resulting shift to the grid pattern is defined as:

\[
\delta x = \sigma^2(-r_1 + 2r_2(x_c - \mu_g))
\] (B.24)

Thus, the shift distance is proportional to the distance between the shift centre \( x_c \) and the grid field peak \( \mu_g \).
B.2.2 Extending to 2D

It has so far been shown that in 1D, applying an exponential-polynomial re-weighting to the PC inputs results in a linear shift to the grid pattern where the shift magnitude is proportional to the distance between the shift centre and the grid field. Extending the previous analysis in 2D, the 2D reweighting function can be defined as:

\[ R = e^{r_1(\mu_p x - c_x)(\mu_p y - c_y)} \]  

(B.25)

Which, following the previous approach gives:

\[
\delta x = -\sigma^2 r_1 (c_y - \mu_y) \\
\delta y = -\sigma^2 r_1 (c_x - \mu_x)
\]  

(B.26) (B.27)

I.e. the shift in the \( x \) direction is linearly proportional to the distance from the shift centre in the \( y \) coordinate (and vice versa), which defines a shearing transformation. The magnitude of the shift is controlled both by the magnitude of the exponential decay in PC density away from the centre \( r_1 \) and the tuning width of the PCs \( \sigma \).

![Fig. B.2: Effect of PC density decay on grid pattern shearing.](image)

B.2.3 Effect of shearing on \( A_{min} \)

The field centres of the unperturbed grid pattern can be defined by the intersection of two basis vectors:

\[ \mu_{ij} = c + \lambda(i\mathbf{v}_1 + j\mathbf{v}_2) \]  

(B.28)

where \( \mathbf{v}_1 = (1, 0)^T \) and \( \mathbf{v}_2 = (1/2, \sqrt{3}/2)^T \) and \( \hat{c} \) is the base spatial offset. Applying the shearing transformation shifts the grid fields such that their new locations are represented by:

\[ \mu_{ij} = c + \lambda(i\mathbf{v}_1 + j\mathbf{v}_2 + \delta x) \]  

(B.29)
where $\delta x = (y\sigma^2 r_1, x\sigma^2 r_1)^T$. $A_{\text{min}}$ can then be calculated from the angles of the two shifted basis vectors.
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