The Hippocampal-Entorhinal Complex performs Bayesian Localization and Error Correction

Tamas Madl[1,*], Stan Franklin[2], Ke Chen[3], Daniela Montaldi[4], Robert Trappl[5]

1 School of Computer Science, University of Manchester, Manchester M13 9PL, UK
2 Institute for Intelligent Systems, University of Memphis, Memphis TN 38152, USA
3 School of Computer Science, University of Manchester, Manchester M13 9PL, UK
4 School of Psychological Sciences, University of Manchester, Manchester M13 9PL, UK
5 Austrian Research Institute for Artificial Intelligence, Vienna A-1010, Austria
∗ E-mail: Corresponding tamas.madl@gmail.com

Abstract

The mammalian brain updates representations of spatial location with self-motion cues, a process referred to as path integration. Since self-motion information is inherently inexact and subject to neuronal noise, this process leads to errors, which would accumulate over time if not corrected by sensory information about the environment.

In this paper, we propose that the hippocampal-entorhinal complex, the major neuronal correlate representing spatial information, corrects such errors by integrating self-motion information and sensory information about the environment in a Bayes-optimal manner. Based on theoretical arguments as well as empirical data, we propose that hippocampal place cells are able to encode probability distributions and uncertainties of allocentric spatial location, and to use them for Bayesian inference to improve the accuracy of the location representation using different sources of information. We hypothesize about possible neuronal correlates of the components and processes required for such inference.

Unlike most previously suggested error correction and spatial cue integration mechanisms, we not only provide a plausible neuronal basis for these mechanisms but also generate concrete predictions from our hypotheses and substantiate them with empirical data. We describe a computational model performing Bayesian localization in arbitrary two-dimensional environments in a biologically plausible way, and use it to replicate neuronal recording data as well as behaviour data in published studies in order to strengthen our claims.

Our approach ties in with a growing body of research suggesting that the brain might behave like, or possibly implement, a Bayesian machine (e.g. the Bayesian brain hypothesis [1]).

Author Summary

Accurate spatial localization requires a mechanism correcting errors arising from inaccurate sensory information or neuronal noise. In this paper, we provide an explanation of how the brain might implement such an error correction mechanism: by integrating different sources of information in a statistically optimal fashion. Behaviourally, this yields specific predictions about the errors that subjects make when deprived of specific sources of sensory information. Neuronally, this suggestion implies that statistical representations should exist in brains. We reproduce behavioural as well as neuronal recording data using a computational implementation of our hypothesis. Our results confirm our predictions and strengthen the idea of statistically optimal localization in the brain.

Introduction

For successful navigation, an organism needs to be able to localize itself (i.e. determine its position and orientation) as well as its goal, and it needs to be able to obtain a route between these locations. Since the first recording evidence for 'place cells' [2], hippocampal cells with spatially selective firing patterns,

there have been a large number of empirical findings supporting the idea that the Hippocampal-Entorhinal Complex (HEC) is a major neuronal correlate underlying spatial localization and mapping [3].

To keep track of their location when they move, mammals must integrate self-motion signals and use them to update their location estimate, using a process commonly referred to as path integration or dead reckoning. The medial entorhinal cortex (MEC) has been proposed to perform this function in a number of theoretical as well as empirical studies [4–6]. Path integration alone is prone to accumulating errors (arising from the inaccuracy of sensory inputs and neuronal noise), which add up over time until the location estimate becomes too inaccurate to allow efficient navigation [7, 8]. Therefore, the output of the path integrator has to be corrected using allothetic sensory information from the environment. It has recently been suggested that the entorhinal path integrator could be corrected using such sensory information, for example via hippocampal back-projections [9–11]. However, the exact mechanism correcting the errors accumulated during path integration is still unknown. Existing models proposing concrete quantitative mechanisms for entorhinal error correction (e.g. [12–14]) are mostly theoretical and, as of yet, their correction mechanism is not substantiated by experimental data. Furthermore, although some broader models unconcerned with exact neuronal mappings and proposing that spatial cognition involves Bayesian state estimation (e.g. [15–18]) have been put forth, they also lack experimental confirmation and, in some cases, plausible neuronal substrates for implementation (see the Discussion section for an overview of related work).

In this paper, we propose that the mammalian HEC performs Bayesian localization to maintain a noise filtered and error corrected spatial location estimate, similarly to state-of-the-art localization algorithms in robotics [19]. We propose that ensembles of HEC neurons represent not only location estimates [5] but also contain information about their uncertainty, and hence are able to incorporate different types of uncertain measurements into the estimate in a statistically optimal fashion. We present a computational model, establish possible underlying neuronal substrates, and list verifiable behavioural and neuronal predictions of our model. We also compare simulation results with rat neuronal recording data as well as human behaviour data to substantiate the model. Finally, we discuss the implications of our results and how they fit in with existing ideas concerning a 'Bayesian brain' [1].

Neuronal Correlates of Localization

Here we briefly summarize neuroscientific literature concerning how mammalian brains represent space. Most of these results come from animal (rat, and to a lesser extent, monkey) cellular recording studies, although there is some recent evidence substantiating the existence of these cell types in humans.

Four types of cells play an important role for allocentric representations in mammalian brains:

1. Grid cells in the medial entorhinal cortex show increased firing at multiple locations regularly positioned in a regular grid across the environment consisting of equilateral triangles [25] (Figure 1 A). Grids from neighbouring cells share orientation, but have different and randomly distributed offsets, meaning that a small number of them can cover an environment. Grid cells have also been suggested to play a major role in path integration, their activation being updated depending on the animal's movement speed and direction [3, 4, 25, 26]. They seem to exist not only in mammals but also in the human entorhinal cortex (EC) [27, 28].

2. Place cells are pyramidal cells in the hippocampus which exhibit strongly increased firing in specific spatial locations, largely independent from orientation in open environments [2, 3] (Figure 1 B), thus providing a representation of animals (or humans [29]) location in the environment. A possible explanation for the formation of place fields is that they emerge from a combination of grid cell inputs on different scales [5, 30] (Figure 3).

3. Head-direction cells fire whenever the animal's head is pointing to a certain direction (Figure 1 C). The primary circuit responsible for head direction signals projects from the dorsal tegmental

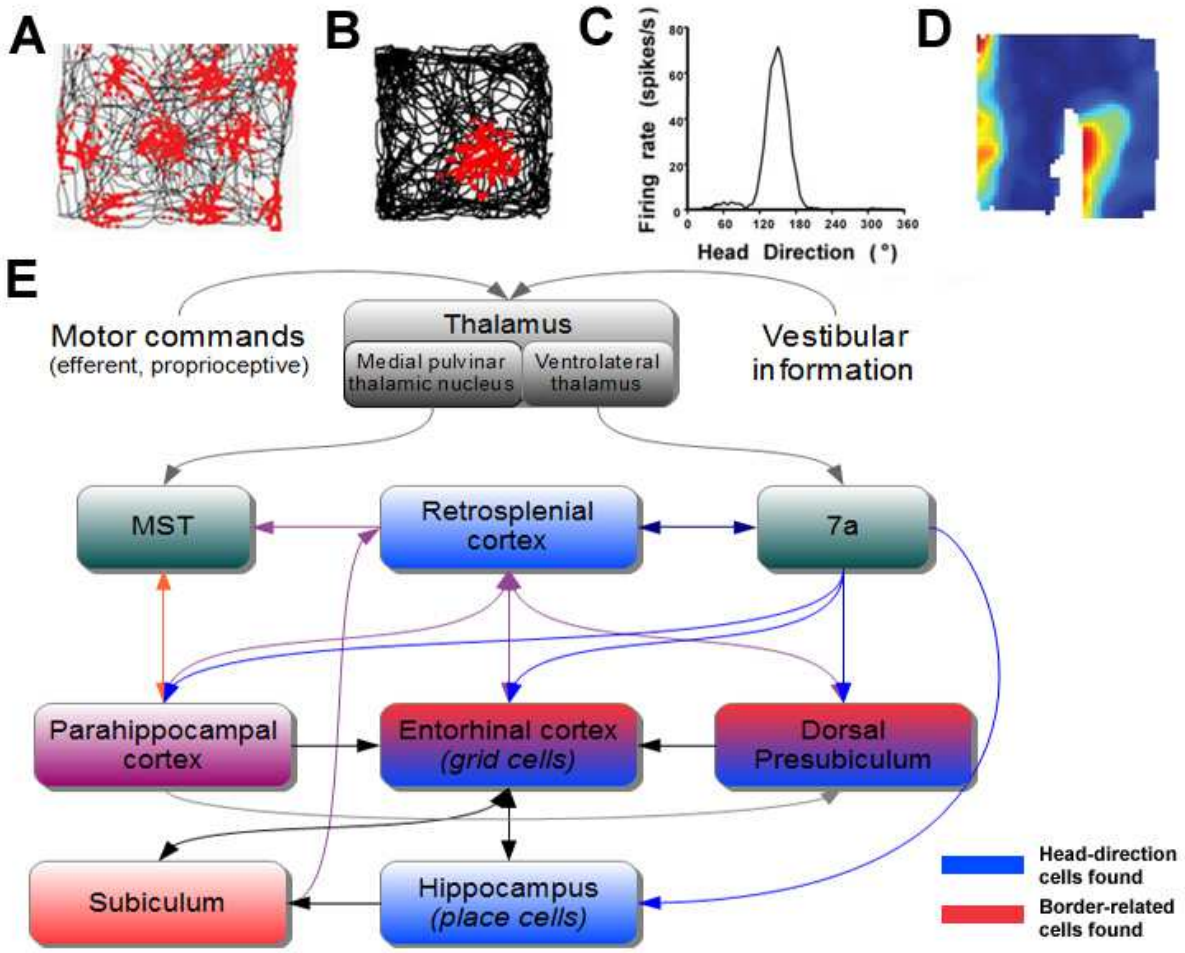

Figure 1. Grid cells, place cells, boundary-related cells, head-direction cells, and the neuronal basis of self-motion information. A. Regular grid cell firing pattern from rat intracranial recording (black lines: rat trajectory, red dots: places where grid cell showed increased firing). B. Hippocampal place cell firing pattern (A and B from [3]). C. Firing pattern of a head-direction cell tuned to about 150 allocentric direction (relative to distal landmarks or boundaries). D. Firing fields of 'boundary vector cells' identified in the rat entorhinal cortex [20]. In specific areas of the environment (highlighted with hot colours) these cells exhibit increased firing rates. (from [20]). E. Connectivity diagram showing the origins and pathways of self-motion information to the HEC and the entorhinal path integrator. Boxes containing lightblue shading represent brain areas where head-direction cells have been found [21], and ones containing red shading show areas where cells with activity related to environmental boundaries have been identified [20, 22, 23]. Diagram adapted from [24].

nucleus to the lateral mammillary nucleus, anterior thalamus and postsubiculum and terminates in the entorhinal cortex [21]. There is evidence that head direction cells exist in the human brain within the medial parietal cortex [31].

4. Cells with boundary related firing properties (Figure 1 D). These include border cells [20, 22] which

seem to fire in proximity to environment boundaries and Boundary Vector Cells (BVC) [3, 23] with firing depending on boundary proximity as well as direction relative to the mammal's head. Cells with these properties have been found in the mammalian subiculum and entorhinal cortex [20, 22], and there is also some behavioural evidence substantiating their existence in humans [23].

Since a large part of this paper is concerned with the correction of errors accumulated by the neuronal path integrator supposedly implemented by entorhinal grid cells [4], we also briefly outline the pathways conveying self-motion information - motor efference, proprioceptive and vestibular - to this brain area (cf. Figure 1 E). Motor-related projections from the motor cortex and subcortical sensorimotor structures reach the thalamus and the striatum and provide efference copies of motor commands [32] (i.e. internal copies of the predicted movement). The thalamus (the ventrolateral and ventro-posterior lateral) also receives vestibular information via the vestibular nuclei, which are mainly activated by the vestibulo-cochlear and vestibular nerves transmitting information from the inner ear, but also receive proprioceptive signals [33]. The pathways of self-motion signals to the hippocampus and the entorhinal cortex are not yet clearly established [34]. Vestibular information could reach the entorhinal cortex (and, subsequently, the hippocampus) by a pathway via the thalamus possibly involving the posterior parietal cortex [34]. There also seem to be sensory-based spatial representations in the medial superior temporal area MST (tuned for optic flow and inertial motion) and area 7a (tuned to head movements) [24], which receive thalamic input and indirectly project to the entorhinal cortex (more specifically, both MST and 7a project to the EC via the parahippocampal cortex, but 7a also directly projects to the dorsal presubiculum and the EC) [24, 35] (see Figure 1).

Please note that we take a highly simplified and constrained view on HEC function and anatomy in this paper. Hippocampal cells play a role in many functions other than spatial localization, among others long-term episodic memory, declarative memory [36], memory based prediction [37, 38], and possibly short-term memory, recognition memory [39] and perception [40]. Furthermore, their role in spatial representations is more complex than our brief description might suggest. For example, place cells convey not only rate-coded information but also a temporal code (in the form of phase precession - place cells firing at progressively earlier phases in relation to the phase of a theta cycle as the animal traverses the place field) [26]. However, we believe that dealing with the described small subset of functionality and anatomy suffices for investigating our central hypotheses.

Results

Probabilistic Models of Localization

Just as biological organisms, autonomous robots also need a mechanism for establishing their location in an environment. In robotics, it was recognized early [41] that some kind of probabilistic estimation method is required to integrate multiple types of uncertain information. Robots need to sense their own movements (odometry), as well as the world around them (landmarks, boundaries, objects, etc.). They need to integrate these sources of information, accounting for their various uncertainties or expected measurement errors, and correcting accumulated odometric errors, in a probabilistic framework [19, 42]. Based on the success of probabilistic methods in robotics, it would be reasonable to expect such a functional mechanism in the part of the brain responsible for self-localization [8].

Bayes' theorem provides a way to update probabilistic beliefs in a statistically optimal fashion. In its basic form, it says that the updated belief in a hypothesis should be proportional to the likelihood of (or degree of belief in) the new information given that hypothesis, prior knowledge about the hypothesis, and a normalization factor (the denominator in equation (1)). Performing Bayesian inference, the probability of a hypothesis H being true, given some data D, can be updated using Bayes' rule:

$$p(H|D) = \frac{p(D|H)p(H)}{p(D)} \tag{1}$$

There is increasing empirical evidence that behaviour produced by the brain is close to the predictions of Bayesian models [1, 43–47]. Bayesian models provide one way to solve the mentioned problem of accumulating errors during path integration. For example, the output of a neuronal path integrator could be treated as a Bayesian 'prior belief' about the agent's position. If the location of a landmark or boundary is known in advance, and that landmark or boundary is perceived at a specific distance, this distance can be used to calculate a more accurate, updated belief (posterior) according to Bayes rule (Figure 2). The more landmarks are perceived, the better the estimate should become. In contrast, depriving the agent of sensory stimuli or decreasing path integration accuracy should result in a worse estimate (see Results).

Improving the location estimate depends on the availability of prior information as well as sensory information about the environment, so possible neural substrates implementing a location estimator should have these inputs. It has been known for over thirty years that this is true for hippocampal place cells. In in his early seminal work on place cells, O'Keefe [51] has written *'...Each place cell receives two different inputs, one conveying information about a large number of environmental stimuli or events, and the other from a navigational system which calculates where an animal is in an environment independently of the stimuli impinging on it at that moment.'* Because of the inputs and the spatial selectivity of place cells, location estimation has long been suggested to be the primary function of place cells. However, the exact mechanism accomplishing this is still unknown.

Here, we propose that the brain integrates available cues in a Bayesian framework on a cellular level, correcting the position estimate from a path integrator (motor model) with perceptual information about landmarks and boundaries (perceptual/sensory model) in a Bayes-optimal fashion (see Methods for details).

A path integration mechanism which could, in principle, perform the function of the motion model has been identified in the entorhinal cortex [4]. Furthermore, hippocampal place cells might represent a probability distribution encoding the current location and its associated uncertainty. We will outline a possible way of uncertainty representation in the HEC in the sections below.

Possible Neuronal Implementation of Probabilistic Localization

As already mentioned above, our main hypothesis is that

1. **The HEC performs Bayesian localization** (see Methods for details)

Furthermore, we tentatively suggest neuronal substrates underlying the components of our Bayesian localization model (note that the main hypothesis does not depend on all of these suggestions).

2. **The belief distribution representing a spatial location might be encoded by means of hippocampal place cells, or ensembles of place cells**. Both the belief and place fields (spatially constrained regions within which a place cell exhibits increased firing) correspond to a specific spatial location [5,8,51]. Furthermore, there is evidence for the assumption that place cells, or ensembles of such, encode a probability distribution, i.e. not only encode a single position but also the uncertainty associated with it. It is becoming increasingly clear that neuronal representations of quantities also need to represent uncertainty associated with them [1, 52–55], and some concrete ideas have been proposed about how the hippocampus might encode uncertainty [56–59]. Place cell firing fields can be modelled by Gaussian distributions in open fields [60, 61], and they also exhibit other properties associated with probabilistic neural codes (e.g. [55]). Finally, properties of place cells, such as their firing rate and their place fields, change in ways similar to probabilistic representations (see Results). These properties have enabled us to compare the uncertainty they might encode to the predictions of our model (see below).

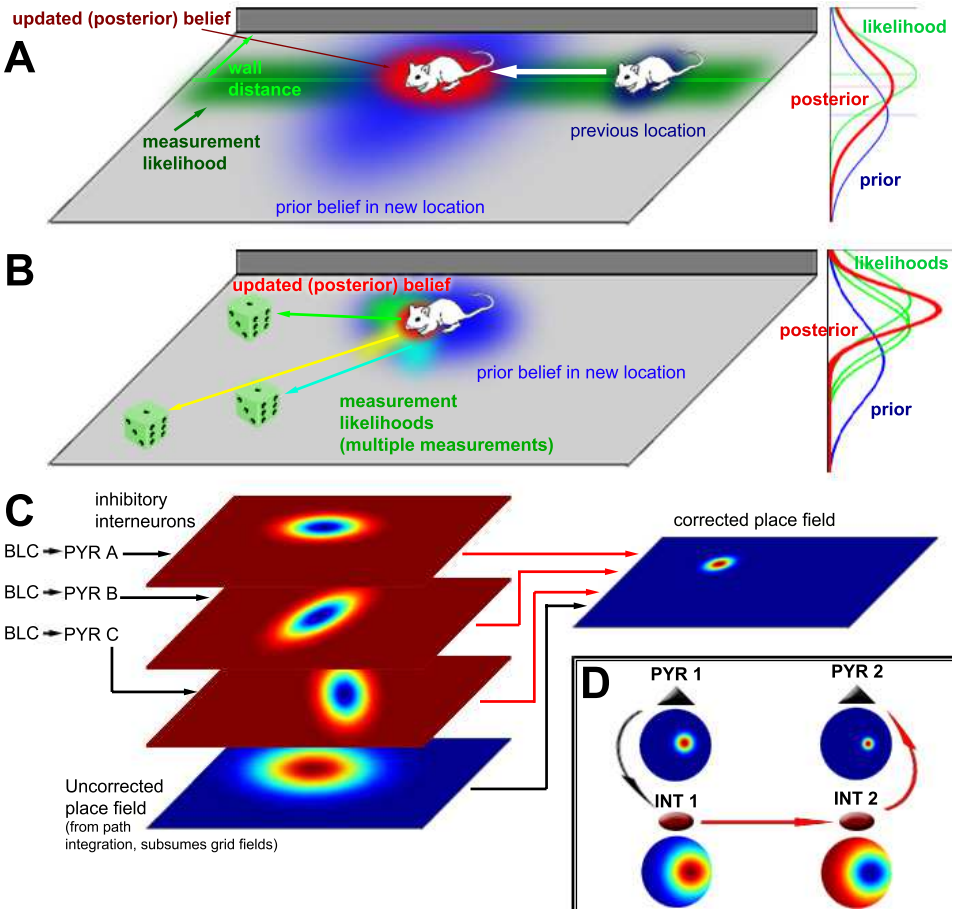

Figure 2. Bayesian location estimation. A. Left: Movements introduce errors in the prior location belief that the path integration system keeps track of (light blue ellipse). The uncertain belief can be improved using a measurement (dark green), e.g. the likelihood that the rat is at a specific distance from the wall, given perceptual information. The resulting posterior belief (red) will be more exact (less uncertain) than the prior belief. Right: Illustration of an improved posterior probability distribution (red) based on a prior distribution (blue) and a likelihood (green). B. Location estimates (prior belief, light blue) can be further improved with additional measurements (e.g. landmark information). More measurements lead to better estimates and less uncertainty. C. Possible neuronal implementation of place field correction. A number of boundary or distal landmark related cells ('BLC'; for example, boundary vector cells or border cells [20, 48]) provide inputs to pyramidal place cells (PYR) in the hippocampus, which in turn excite interneurons. The bottom place field illustrates the uncorrected belief or position estimate from the entorhinal path integrator. A hypothetical place cell excited by this belief place cell and inhibited by interneurons with place fields dependent on various environmental features could represent a corrected position estimate (since the parts of the uncorrected place field inconsistent with environmental features will be removed - the cell will not fire there - due to the inhibitory interneurons). Hippocampal back-projections to the EC [9–11] could also contribute to the error correction in a similar fashion. D. Spatial correlation data between pyramidal cell and interneuron firing [49, 50] indicates that interneurons (INT) excited by pyramidal cells (PYR) might in turn inhibit other interneurons and pyramidal cells (excitatory connections: black, inhibitory connections: red). This could provide a mechanism for place field error correction.

3. **The motion model might be implemented by the entorhinal path integrator.** Entorhinal grid cells, one synapse upstream of the hippocampus, are one of the sources of spatial inputs to hippocampal place cells. Their activity forms a regular grid of firing fields, and is updated whenever an animal moves [4]. This observed functional property, along with anatomical connectivity (vestibular and idiothetic inputs into the entorhinal cortex, see Introduction), suggests that grid cells might implement path integration [4, 5]. Studies investigating the effects of entorhinal lesions (e.g. [62]) are consistent with the role of the EC in path integration [7, 8] and, since they show that such lesions substantially reduce place cell firing rate, as well as field size and stability [62], as predicted by our model [1], strengthen our claim of uncertainty being encoded by place cells.

4. **Noise and uncertainty accumulated by the path integrator might be corrected by means of interneuron inhibitory dynamics**, in a Bayes-optimal fashion (taking into account the different measurement and path integration uncertainties). There is some evidence that inhibitory interneuron inputs to place cells contribute to and constrain hippocampal place fields [49, 50]. Empirical experiments suggest that interneurons are necessary for normal spatially constrained place fields [63], and that they might gate entorhinal inputs [64]. These properties make it possible to correct the belief encoded in place cells (see Figure 2).

5. **The perceptual model might be partially encoded by spatially selective cells in the subiculum and the entorhinal cortex.** Recently, cells with activities depending on the distance to environmental landmarks or boundaries, so-called border cells and boundary vector cells, have been reported in the subiculum and entorhinal cortex [20, 48, 65, 66]. Some of their firing fields resemble oriented Gaussian response functions tuned to the distance and orientation to an environmental boundary [65, 66]. Such cells might facilitate the inference of a spatial location based on sensory distance and orientation information.

   Note that this suggestion is highly tentative. Boundary vector cells (BVCs) have only recently been discovered [20], and part of the small amount of what is known about them is disputed (while [20, 65, 66] propose that BVCs provide inputs to place cells and contribute to the formation of place fields, properties of anatomical connectivity between the subiculum and the hippocampus cast doubt on this claim [48]). There might also be different cells better suited for landmark representation (e.g. spatially selective postrhinal cells [67]). For this reason we cannot provide a solid explanation of how the perceptual model might be implemented neuronally. However, the predictions and claims in this section and our simulation results do not depend on the existence or function of BVCs - they are only contingent upon the existence of a mechanism that correlates hippocampal place cell and interneuron firing fields with sensory measurements of landmarks and boundaries, a condition which has been thoroughly verified empirically [3].

Model Predictions

The assumption that spatial uncertainty is correlated with place cell firing rates and place field sizes, and the hypothesis that the HEC performs Bayesian localization, can be used to generate specific and testable predictions of our model:

1. **Place cell firing rate increases with movement speed**, since the major input to CA1 is provided by multiple grid cells, and greater location uncertainty results in more active grid cells. Position uncertainty, measured as the standard deviation of the belief probability distribution, increases linearly with speed in our model (for simplicity, although our main hypothesis does not

[1] Removing the motion model might remove a major source of noise and thus seemingly reduce uncertainty, but will result in unstable position predictions, since it is not always possible to accurately estimate positions based only on the sensor model - see Methods

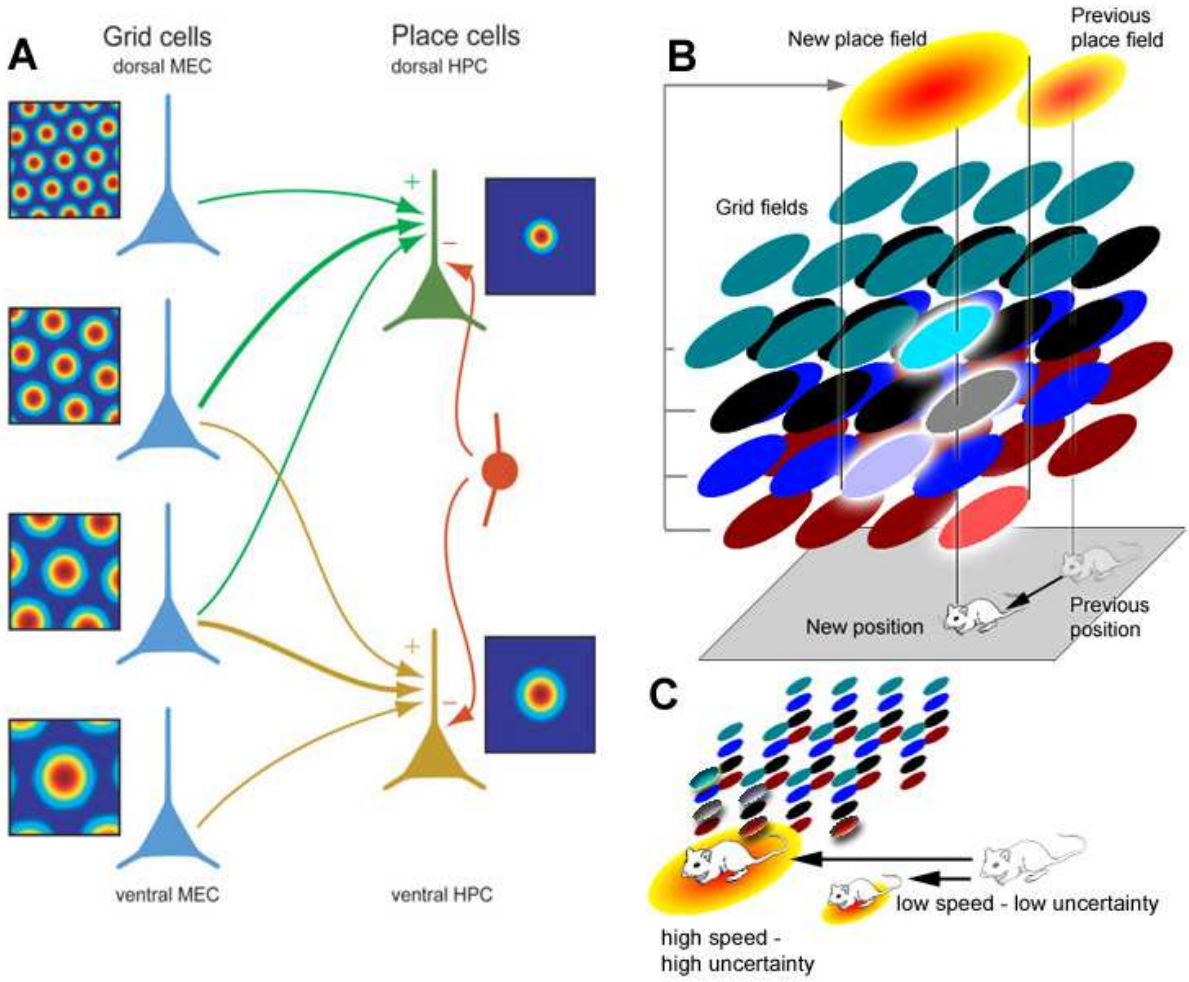

Figure 3. Place fields and uncertainty. A. Grid cells have been proposed to be the main contributors to the formation of place fields (panel A from [30]). B. A place cell will fire when grid cells connected to it are active - the size of its place field will depend on the grid fields of active grid cells[1]. Therefore a path integration error, resulting in active grid fields that are displaced from the true location of the animal, will presumably increase the place field size as well as the firing rate (since the cell receives more input spikes from a large number of widely distributed grid cells than from few spatially constrained grid cells). C. Higher movement speeds result in higher uncertainty (and in a larger spread of grid fields, and thus larger place cell firing rates and fields [68–71]).

require a linear relationship). Since LFP (local field potential) power depends on firing rates, **LFP power in some frequency bands also increase with movement speed**.

2. **Increasing the number of landmarks available for orientation decreases place cell firing rate, as well as place field size**, since more observations result in less uncertainty in a Bayesian framework (see Figure 2)

3. **Experimental conditions depriving mammals of sensory information result in decreased behavioural accuracy**, and, since these sources of information are hypothesized to be integrated in a Bayesian fashion, the relationships between behavioural accuracies with only self-motion information or only sensory information or both can be predicted by a Bayesian model.

Although we will try to infer an uncertainty representation from single-cell recordings in the sections below, due to the availability of empirical data, it is probable that an ensemble of place cells, not just a single cell, is required to fully represent a spatial location [72, 73] and its uncertainty. This does not decrease the plausibility of single place cell activity being correlated to uncertainty (and location), which is one of our assumptions, and which we will try to empirically substantiate below (also, substantial evidence supports the argument that single place cell activity is influenced by an ensemble of entorhinal cells [5, 6, 30], and thus does not contradict 'ensemble coding' hypotheses).

Note also that we do not claim that there is a decodable one-to-one relationship between the mentioned probability distributions, or their uncertainty (e.g. standard deviation), and firing rates or field sizes.[2] Many empirical observations would make such a claim implausible. First, there is a large number of uncertainty-unrelated factors influencing firing rates and place fields (e.g. the colour of the environment, or recent experience, or future actions [5, 38, 75, 76]). Second, these properties are not homogenous in the hippocampus. For example, the scale of place fields significantly increases from < 1 meter at the dorsal pole to 10 meters at the ventral pole [77] (an increase also observable in the entorhinal cortex [78]); and firing rates are significantly different between different layers and cell types in the hippocampus [79]. These observations would make it very difficult to map uncertainty to these properties (e.g. to devise an equation or model mapping firing rate or field size to location uncertainty). However, they do not contradict the assumption that these neuronal properties are correlated to uncertainty, and that they can be different when environmental conditions change, given that they are recorded from the same cell. This is our underlying assumption when comparing our model with recording data. Note further that we are not trying to generalize any of these claims to *all* cells of a given type or of a given brain region. We are merely trying to show that there is a subset of the cell types mentioned above with properties substantiating our hypothesis.

We have implemented Bayesian location estimation according to equation (6) (see Methods), and have used this implementation to simulate different published experiments (closely reproducing the environment and conditions used) and to compare the resulting data to strengthen our hypotheses. We conducted two types of simulations: replications of neuronal recording data from rats, and replications of behaviour data from humans (see below). We argue that the results of these simulations substantiate the hypothesis of HEC localization following Bayesian principles.

Simulation results - neuronal representation

This section shows simulation data for testing the predictions listed in the previous section. All described experiments were performed in a simple simulated two-dimensional environment. Although some simplifications have been made, the environment was designed to match the one used in the rat experiments (the distances between objects, as well as animal running trajectories, are the same in the simulation as in the experiment). Since the specific relationship between possible neurally encoded uncertainty and the actual uncertainty of a probability distribution (i.e. the standard deviation) is unknown, we have used scale factors in the presented graphs to enable comparison (one per graph). Despite these factors being somewhat arbitrary, the same factor was used for all different conditions and data points in a graph. This

[2] Figure 3 oversimplifies the place field formation mechanism to illustrate our point. Place field formation might not be a mere 'addition' of grid fields as the figure might suggest (although it has been hypothesized that place cells could be formed by linear summation of weighted entorhinal inputs [30]). Furthermore, place cells still exhibit spatial firing without entorhinal inputs - although the firing patterns become unstable - presumably based on cortical sensory input about the environment as well as 'predictions' from CA3 in familiar environments [62, 74].

means that although the absolute values might differ, the relations, relative slopes, and function shapes observed in the neuronal recordings were accurately reflected by the model.

Place cell firing rate increases with running speed

This prediction follows directly from hypothesis 3. It depends on the existence of a noisy path integrator accumulating errors that depend on movement speed, and on spatial uncertainty being measurable by cell recordings (although not on Bayesian belief correction).

The entorhinal path integrator has to be subject to noise and errors and that these accumulate over time [7,8,80] (otherwise mammals would have perfectly accurate idiothetic or vestibular senses and could find their way back to a shelter or food cache equally well under normal conditions and deprived of sensory input, e.g. in total darkness). As mentioned above, entorhinal grid cells also provide an important input to place cells. These properties imply a correlation between position uncertainty and firing properties of place cells (Figure 3), which have been empirically confirmed: place cell firing rate [68,69], LFP [71], and place field size [70] all increase with increased movement speed of the animal. Furthermore, place cell firing rates and place fields are without entorhinal inputs, which has been confirmed in lesion studies (e.g. [62]).

The linearly increasing uncertainty predicted by our simple model has been observed in the dorsal CA1 region of the hippocampus (Figure 4, left panel). The recording data was obtained from rats running on a circular track containing a barrier with food containers on either side to motivate the rats to keep running.

Consistently with prediction 1, both the standard deviation of the position in the model and dorsal CA1 place cell firing rates seem to increase with movement speed. The relationship seems to be approximately linear in this brain region [3].

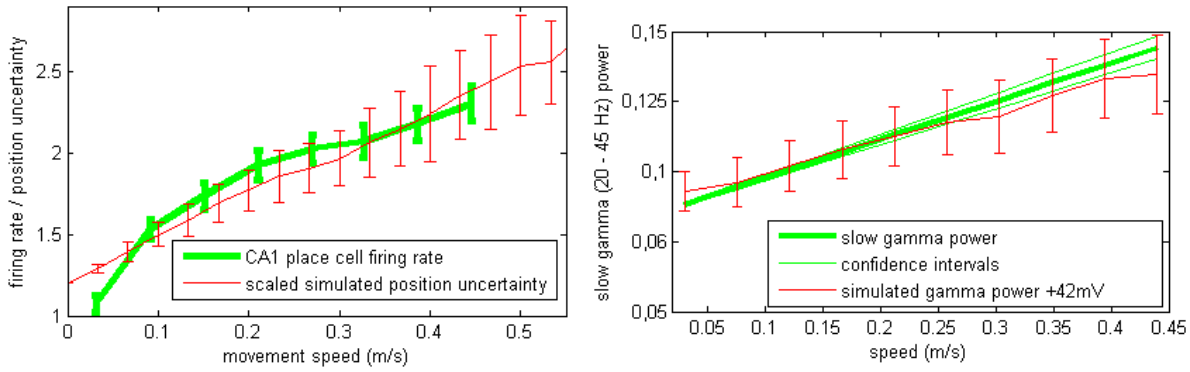

Figure 4. Hippocampal firing rates and gamma power increase linearly with movement speed, as does the uncertainty predicted by the model. Left panel: rat CA1 place cell firing rates (data from [69]), and the position uncertainty in the model running in the replicated environment. Right panel: rat hippocampal slow gamma LFP (data from [71]), and the power spectrum calculated from the model under the assumption that there is a linear relationship between position uncertainty and place cell firing rate.

[3]This can be significantly different in other regions and other cell types - for example, middle CA1 place cells seem to stop increasing their firing rate beyond 15cm/sec [69]. We are not trying to imply that any of our claims are generalizable to multiple cell types or areas. Note further that although our model assumes that uncertainty grows with movement speed, this relationship need not be linear; our main hypothesis could also support non-linear uncertainty relationships. We have assumed this relationship to be linear for simplicity in our concrete implementation (see Methods), and have included this recording data in order to justify our choice.

LFP power in some frequency bands increases linearly with running speed

The curve and scaling factor in Figure 4 can be used to predict local field potential (LFP) power in the hippocampus depending on movement speed. Using the power spectrum (calculated from the Fourier transform [4]) of a spike train [81]. The power spectrum in the slow gamma range (20-45 Hz) of the fitted model results yields a similar curve to empirically observed hippocampal LFP's in running rats (Figure 4, right panel). Adding 42mV background activity (hypothesized to be unrelated to position uncertainty - even a stationary rat in a very well known environment exhibits hippocampal LFP's greater than zero) results in a good match between the model and observed LFPs. (Without added background activity, the slope of the predicted gamma power still matches that of the observed gamma power function, but the absolute values differ).

Increasing the number of landmarks available for orientation decreases place cell firing rate, as well as place field size

To substantiate the plausibility of a Bayesian state estimation model, the prototype implementation was tested on a similar environments as rats in the experiment conducted by [82]. In the experiment, rats were running in circles on a circular track with 106cm diameter, which contained 2 food trays to motivate the rats, and no objects in one condition and 8 pseudorandomly distributed, different objects in another condition.

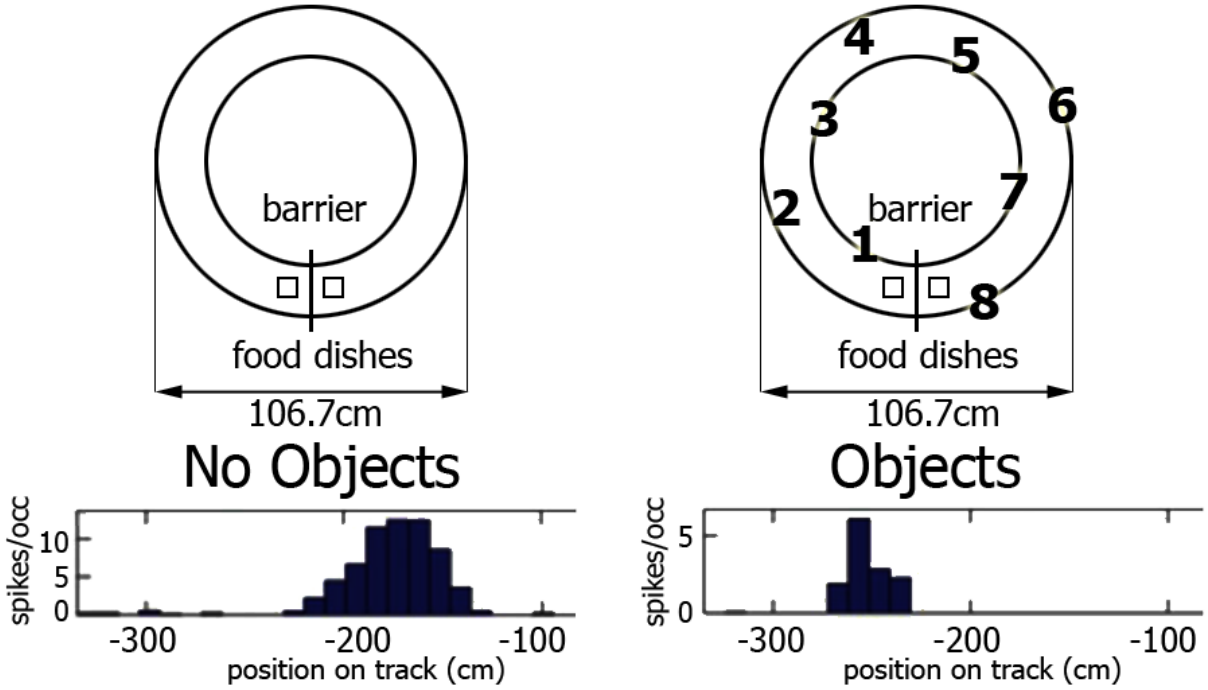

Figure 5. Illustration of the experiment environment, and recordings from two CA1 pyramidal neurons under the no objects (only food trays) and 8 random objects conditions. Place fields were significantly smaller in the condition with objects. (Adapted from [82])

The Bayesian state estimator model was run on a simplified simulation of this environment, and compared to intracranial recordings obtained from the rat.

[4] $P(\omega) = \frac{1}{T}|\int_{-T/2}^{T/2} S(t)e^{-i\omega t}dt|^2$, where S represents the spike train and ω the frequency [81]

Figure 6 (left) shows the simulated relationship between the number of objects available for localization and the position uncertainty (hypothesized to correlate with firing rate). The relationship is non-linear and dependent on the layout of the objects and when / how long they are visible on the circular track. The original paper has only published the object and no-object conditions [82], which are overlain in the graph.

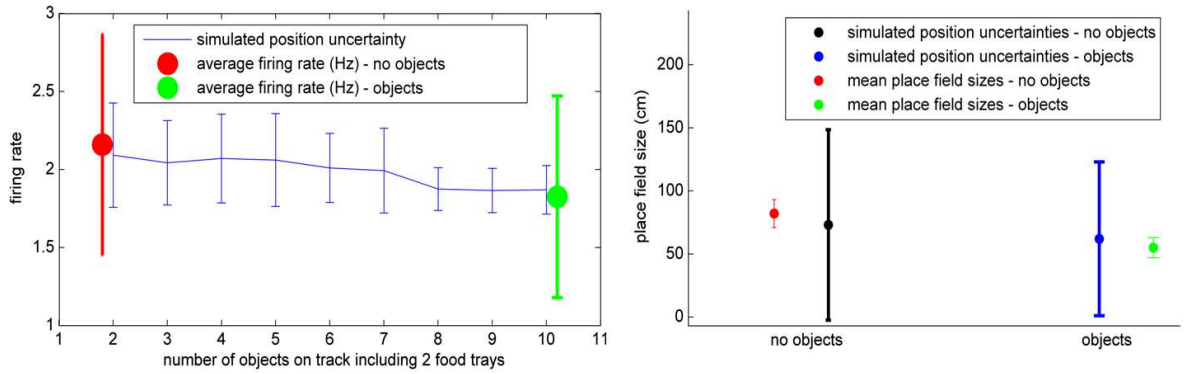

Figure 6. CA1 place cell firing rates and place field sizes, and scaled simulation uncertainties, in the no-objects (red) and objects (green) condition in the [82] experiment. In the 'no objects' condition, the rats (and the software agent) could only see the two food trays, and in the 'objects' condition it could see the two food trays and eight objects. Data from [82].

Place cell firing rates are influenced by a wide variety of factors, including environmental geometry (borders), distal (and, to a lesser degree, proximal) landmarks, non-spatial stimuli such as wall colour, previous recent and memories. Place field sizes are, perhaps, a better way of inferring position uncertainty from recording data. Figure 6 (right) shows place field size data from [82] compared to the simulated uncertainty in the objects and no-objects conditions (the relationship between the object number and simulated uncertainty is the same as in the left panel).

Since approximately reproducing the ratios of firing rates and place fields is by itself insufficient to substantiate the model, we have attempted to reproduce the recorded frequency distributions of different place field sizes (hypothesized position uncertainties) in the model. Figure 7 shows the results.

The apparently chi-square distributed place field sizes already strengthen the claim that place fields might correspond to uncertainties, since uncertainties in path integration models subject to Gaussian noise should be distributed according to a sum of Gaussians [5] (which is a chi-square curve).

Three apparent matches between the simulation and the recording data in Figure 7 strengthen the hypotheses presented above:

- The apparent match between the recorded place field frequency distribution curve and the simulated uncertainty curve, both of which resemble chi-square distributions
- The matching ratio of the most frequent place field sizes / uncertainties in the simulated and recording distributions, at place field sizes 21cm (no objects) and 38cm (objects), respectively; and

[5] One step with random noise would yield a single Gaussian for the uncertainty distribution. Multiple steps accumulate noise, with each step corresponding to different levels of uncertainty, and thus recording all uncertainties at each step over multiple runs will yield a sum of Gaussians. It has been argued that neuron conductivity fluctuations and synaptic noise can be approximated by Gaussian noise [83]

- The roughly matching ratio between all normalized frequencies of occurence between objects and no objects conditions in both the simulated and recorded frequency distributions.

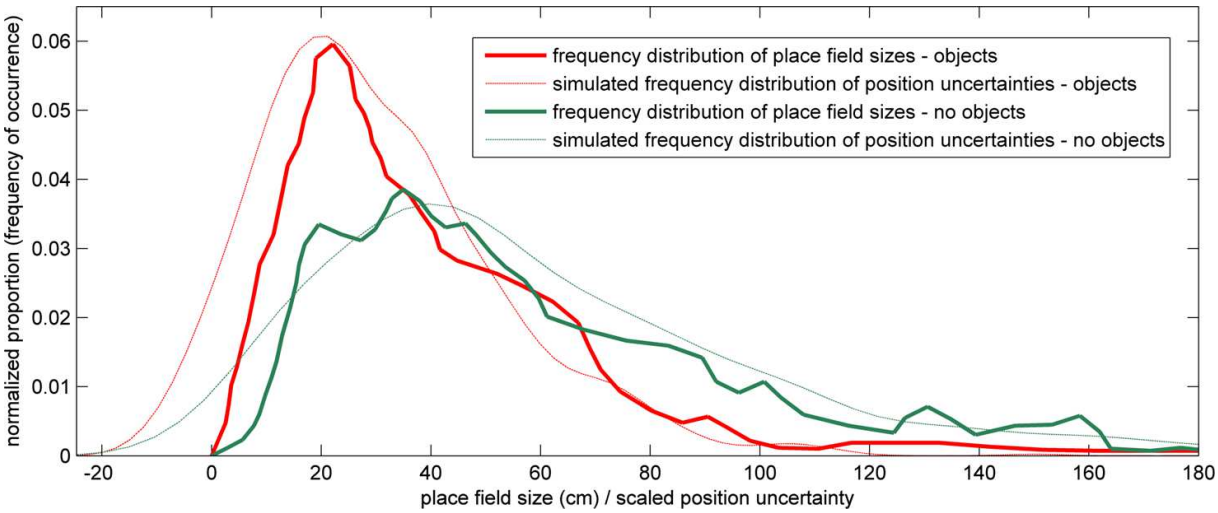

Figure 7. Occurence frequencies of different place field sizes in all measured neurons in the no objects (blue) and 8 objects (red) conditions, compared to the frequencies of position uncertainties in the simulation. Data from [82].

Simulation results - behavior

Experimental conditions depriving mammals of sensory information result in decreased behavioural accuracy

To further substantiate our model, we have replicated a behavioral experiment [84] investigation the integration of self-motion and sensory information in location estimation. In this experiment, subjects were asked to pick up a series of glowing objects in a dark room and to subsequently return the first object to its original location. In one condition, there were three landmarks available for orientation, and subjects were not disoriented - both sources of information were available (self-motion+landmarks). In the landmarks condition, subjects were disoriented by turning to deprive them of orientation information. In the self-motion condition, subjects were not disoriented but the landmarks were turned off. To simulate this experiment, the same environmental layout (with accurate object distances) was reproduced in a simulation. The models parameters were adjusted using a coordinate ascent algorithm. Figure 8 shows the simulation results, which are consistent with the empirical data for adult subjects [6].

[6]Interestingly, this is not the case for young children (4 - 8 year old), who seem to alternate between using either sensory or self-motion information instead of integrating them [84]. This result seems to suggest that the network facilitating cue integration requires a developmental period, and that before the completion of this period there is a conflict detection mechanism in place that simply suppresses the more unreliable source of information (possibly by suppressing that input to place cells). Such conflict detection mechanisms have been suggested e.g. in area CA1, which was hypothesized to perform comparisons between CA3 neurons, performing prediction, and the sensory reality arriving via the entorhinal cortex [85]

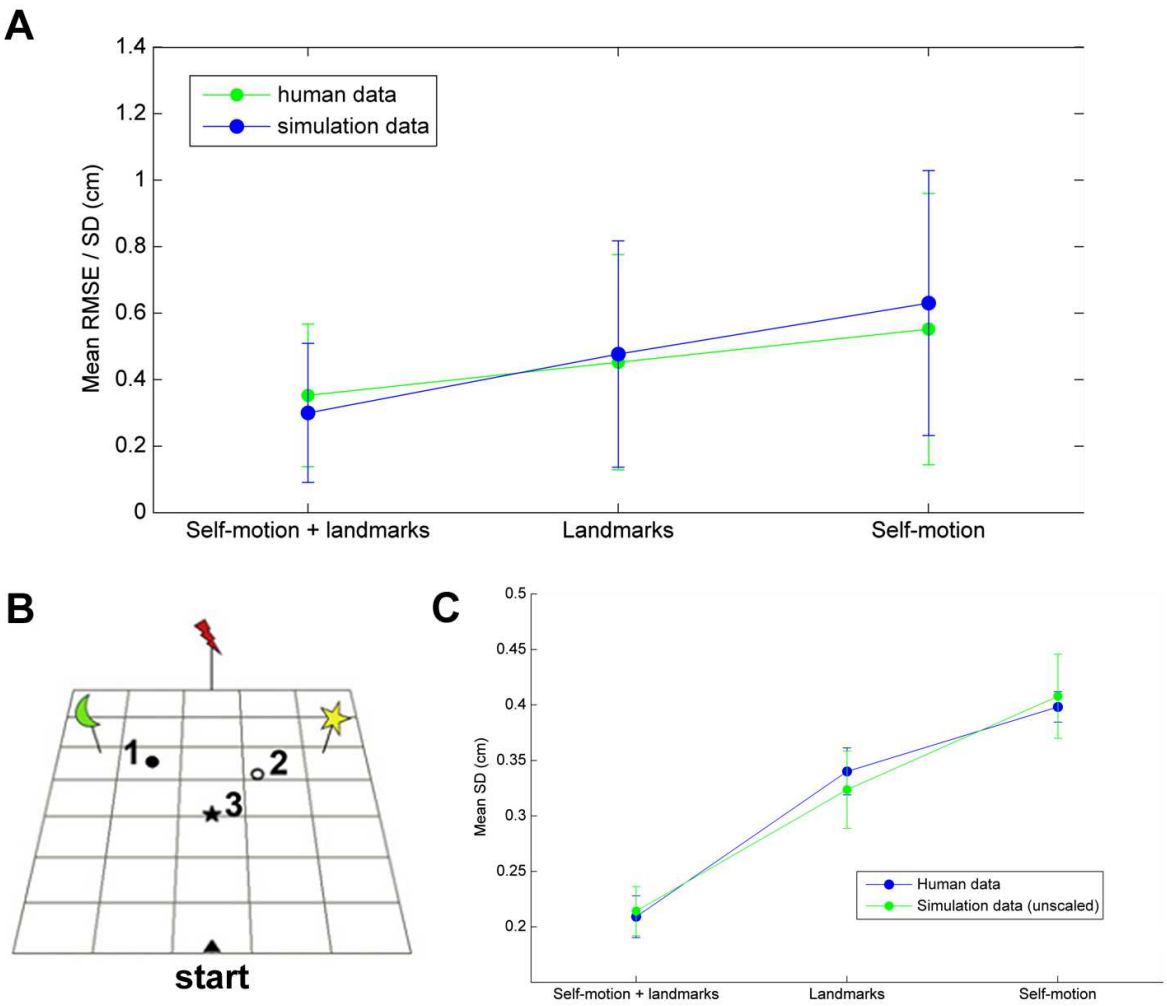

Figure 8. Position errors and standard deviations in the Nardini experiment [84]. A. Mean RMSE (root mean squared errors) of participants, and mean SD (standard deviation), for the responses of human subjects (green) and the agent (blue), respectively. (Since the agent's responses were unbiased, its response location RMSE equals the response location SD). B. The experiment environment. Participants had to pick up objects 1-3 in order, and then replace object 1. The colored objects (moon, star, lightning) are the landmarks. (From [84]). C. Mean SD of participants (green) and the agents (blue)

Discussion

The above theoretical and simulation results strengthen the claim that the hippocampal-entorhinal cortex performs Bayesian localization, and support a novel explanation of location error correction, required to counteract accumulating path integration errors.

It has been suggested early [86] that sensory information might be used to correct path integration error. Previous work building on this idea can be categorized into high-level models, suggesting correction

mechanisms but unconcerned with the details of neuronal implementation, and neuronal-level models. High-level models of hippocampal error correction have proposed a Bayesian information integration mechanism before [15,16,18,46]. [46] propose that spatial information is integrated in a Bayesian fashion, without suggesting a formal model or a neuronal implementation, and provide some behavioural evidence for this claim. [18] suggest Bayesian cue integration to estimate spatial orientation under uncertainty, suggesting Kalman filters (which use unimodal Gaussian probability distributions) or, alternatively, particle filters (which are capable of dealing with multimodal and non-Gaussian probability distributions) as the mechanistic implementation. [15] also hypothesize spatial information integration to be Bayesian, choosing Kalman filters as their implementation.

Kalman filters are possible to implement on biologically plausible attractor networks [14], although they have the disadvantage of being unable to deal with multimodal, non-Gaussian distributions, which can easily arise due to angular noise [1]. Taking a different approach, [12] have used a recurrently interconnected attractor network to correct path integration errors, using sensory information via hippocampal back-projections. Their model, like most attractor-based path integration models, relies on all-to-all interconnections. Extending their ideas, [13] have attempted to map the hippocampal formation onto a Temporal Restricted Boltzmann machine (and argue that inference in their model resembles particle filtering), also modelling on a functional level but trying to adhere more closely to anatomical connectivity. Like the previously mentioned concrete computational models, they do not model empirical data to substantiate their model.

Using oscillatory interference theory instead of an attractor model as their theoretical basis, [87] also use cue-driven feedback to correct location errors and to handle cue conflicts. They also reproduce partial remapping in an experiment, strengthening the mechanism the model uses to resolve cue conflicts.

Building on previous ideas, we have suggested a high-level mechanism (Bayesian localization), provided a computational implementation of the mechanism, and also outlined a possible neuronal-level implementation. Furthermore, unlike most previous suggestions, we substantiated our model with empirical data from both neuronal recording and behavioural studies.

Our results concerning Bayesian localization are an extension to a growing trend in theoretical neuroscience, namely that the brain behaves like a Bayesian machine [43–47], or, in a stronger form, that the brain uses Bayesian inference and probabilistic representations on a mechanism level.

Many researchers are more cautious in their claims, refraining from stating that the actual mechanism behind the brain's sensory system is Bayesian (e.g. [43, 46, 88, 89]). The claim that perception *is* Bayesian inference, implemented physically as a neuronal mechanism, has been criticized due to multiple reasons [89]: the lack of strong neuronal recording evidence in favour of the Bayesian hypothesis (most existing evidence is behavioural, coming from 'Bayesian psychophysics' [89–91]), the arbitrary choice of prior functions in favour of simplicity in many of these models (instead of the choice being based on empirical data), and the possibility to explain Bayes-optimal perception in cue integration (the most widely used paradigm to show Bayesian-optimal behaviour) *without* a Bayesian mechanism by implementing reinforcement learning [88].

In contrast, in this paper we have argued that not only does behaviour conform to Bayesian principles, but that some properties of HEC neurons also seem to resemble the outcomes of Bayesian inference processes. Following the advice of [92] we have generated quantitative experimentally testable predictions, and compared them with empirical results. Thus, as opposed to the view that *'Bayesian models do not provide mechanistic explanations currently, instead they are predictive instruments'* [89], we provide one of few existing pieces of empirical evidence (e.g. [93–95]) that the brain represents uncertainty on the neuronal level, and that there are some neuronal level mechanisms which seem to conform to Bayesian principles. Our model contributes to the *'current challenge for these models [is] to yield good, clear, and testable predictions at the neural level, a goal that has yet to be satisfactorily reached'* [89].

Note that although our results strengthen our hypothesis about Bayesian localization, they do not constrain how exactly uncertainty is represented (the hypothesis itself is independent of the representation

mechanism, although our model implementation is contingent upon certain properties, e.g. that grid cells are the major contributors to place fields - see Results section). Many ways of how the brain could represent uncertainty have been proposed, and reviewing them here would exceed the scope of this paper (see [53, 55] for recent reviews).

Methods

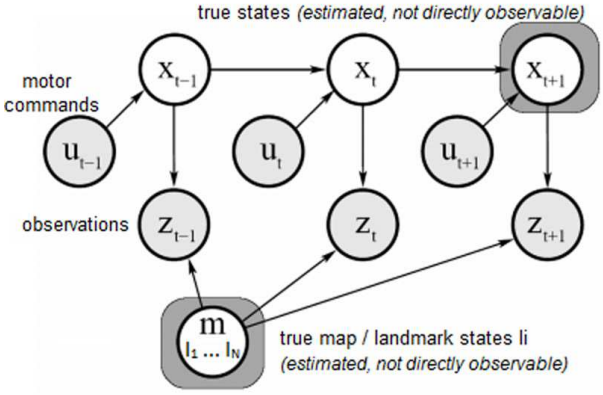

Figure 9. Bayesian Network representing the localization problem. Variables shaded in grey (motor commands and measurements) are observable, those with a white background are not directly observable and have to be inferred (true locations and true map)

The localization problem can be formulated as a Bayesian network consisting of true states (i.e. positions and orientations) in an environment, the states of the objects of the environment, and motor commands and sensory observations (see e.g. [42, 96] and Figure 9). The latter two are the only metric information directly available to the agent[7]; the true states of landmarks and of the agent itself are not directly observable and have to be inferred from them.

By 'Bayesian Localization' we mean the estimation of the posterior probability distribution of the true state x, in other words the belief in the agent being located at x in the environment, based on motor command and sensory information.

After t timesteps and given N landmarks or objects in the environment, this belief is

$$Bel(x_t) = p(x_t|u_{1:t}, z_{1:t}, l_{1:N}) \tag{2}$$

specifying the probability distribution of the current position x_t given motor commands u, measurements z, and landmarks l. This expression can be expanded using Bayes' rule,

$$Bel(x_t) = \eta p(z_t|x_t, l_{1:N}) p(x_t|u_{1:t}) \tag{3}$$

and further expanded by integrating over the state at time $t-1$

$$Bel(x_t) = \eta p(z_t|x_t, l_{1:N}) \int p(x_t|x_{t-1}, u_{1:t-1}) p(x_{t-1}|u_{1:t-1}) \mathrm{d}x_{t-1} \tag{4}$$

[7]We will use the term 'agent' in arguments which we suggest might apply for biological agents (organisms) as well as artificial agents (robots, software agents).

Using the Markov independence assumption (assuming that the current state sufficiently represents all previous states), which means that $p(x_t|x_{t-1}, u_{1:t-1}) = p(x_t|x_{t-1}, u_{t-1})$,

$$Bel(x_t) = \eta p(z_t|x_t, l_{1:N}) \int p(x_t|x_{t-1}, u_{t-1}) p(x_{t-1}|u_{1:t-1}) \mathrm{d}x_{t-1} \tag{5}$$

and because $Bel(x_{t-1}) = p(x_{t-1}|u_{1:t-1}, z_{1:t-1}, l_{1:N})$,

$$Bel(x_t) = \eta p(z_t|x_t, l_{1:N}) \int p(x_t|x_{t-1}, u_{t-1}) Bel(x_{t-1}) \mathrm{d}x_{t-1} \tag{6}$$

This recursive belief update equation [42] is a Bayes-optimal solution to the localization problem and in principle allows for the estimation of the state based on two conditional densities: the motion model or forward model

$$p(x_t|x_{t-1}, u_{t-1}) \tag{7}$$

specifying the effects of a motor command on the state, and the perceptual or sensor model

$$p(z_t|x_t, l_{1:N}) \tag{8}$$

specifying the probability distribution of a given measurement z_z at a position x_t given the landmarks $l_{1:N}$.

We have already hypothesized about the underlying neuronal substrates of the sensory and motion model in the Results section. Below we shall describe our computational implementation of equation (6) in a very simple two-dimensional environment.

We have used a particle filtering (sequential Monte Carlo) approach [42] to estimate the belief probability distribution. This means in essence that the belief distribution representing the location is sampled using multiple location hypotheses. The mean of these hypotheses corresponds to the 'best guess' estimate, and their standard deviation to the associated uncertainty.

Each particle (hypothesis), is updated regularly using self-motion information (linear and angular movement speed) according to the motion model (7), which performs simple path integration:

$x_t = x_{t-1} + v'\Delta t$ at simulated timesteps Δt. Gaussian noise is added to the true speed to simulate noisy vestibular and idiothetic pathways and sensors:

$v' = v_{true} + \mathcal{N}(1, Q)$, where $Q = \begin{bmatrix} \sigma_v^2 & 0 \\ 0 & \sigma_\omega^2 \end{bmatrix}$,

and σ_v^2 and σ_ω^2 are the variance parameters controlling the amount of noise added to the linear and angular speeds, respectively (it has been argued that neuron conductivity fluctuations and synaptic noise can be approximated by Gaussian noise [83]). Without a correction mechanism, this would lead to a gradual uncontrolled increase of uncertainty and the corruption of the belief distribution represented by the set of particles.

To correct this distribution, and to estimate the target posterior distribution (2), each particle is weighted according to the likelihood of the perceived sensory measurements from the location hypothesis represented by the particle, i.e. according to the sensor model: $w_t^i = p(z_t|x_t^i, z_{t-1}, u_t)$. This approach of estimating a target distribution is called importance sampling (see e.g. [42, 96] for the derivation).

After the weights have been calculated, a new set of particles (hypotheses) has to be generated based on the probabilities derived from the sensor model. This is called resampling in the Monte Carlo literature. Usually, resampling is done by drawing with replacement from the old particle set with probabilities proportional to the particle weights [42, 96]. Since drawing with replacement involves a copying mechanism multiplying high probability hypotheses, and such a mechanism is unlikely to operate on short enough time scales in the HEC (although it could, theoretically, be implemented, by Hebbian learning for instance), we have taken a different approach in the simulation used to generate the graphs in the Results section. We simply discard some of the weakest particles in a probabilistic way, with a

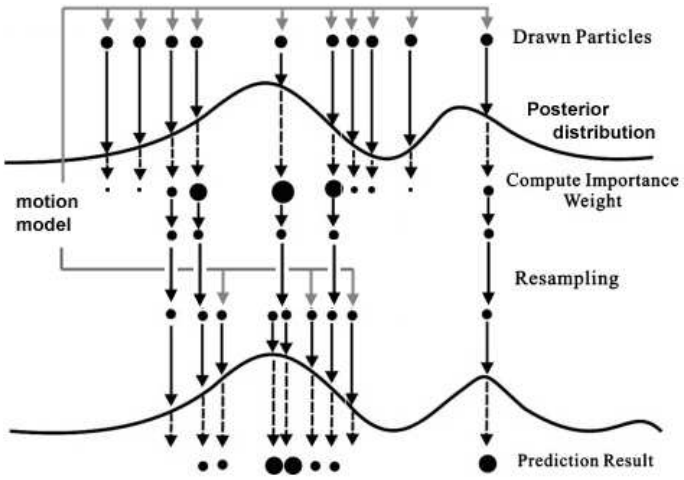

Figure 10. Monte Carlo Importance Sampling. Distributions that can not be conveniently sampled (in this case the posterior distribution representing the location) can be approximated by sampling from a known proposal distribution (in this case, the motion model), weighting the samples or particles (by the sensor model) and resampling to reflect the weighting and improve the approximation. Filled circles represent particles, and their size the particle weight. Adapted from [97]

probability inversely proportional to their weight, and replace them with new particles (novel hypotheses) generated using the motion model. Just like the replacement drawing approach, this mechanism leads to slowly decreasing uncertainties in stationary agents repeatedly observing the environment, and to increasing uncertainties in moving agents because of accumulating path integration error; a phenomenon we have made use of for comparisons in the Results section. There is no substantial difference in the behaviour of the system between using these two resampling approaches [8].

The perceptual model can be implemented in a large number of different ways [42], and the exact implementation is not important for our hypotheses (all they require is a mechanism to 'rate' or weight particles or location hypotheses based on sensory input). In our implementation, we used a simplified two-dimensional occupancy grid [98], which the agent uses to remember landmarks. Whenever a landmark is perceived to be in a specific grid cell, the probability that this cell is occupied is increased. This leads to a possibly multimodal probabilistic representation of landmark locations; using Gaussian noise, the grid will contain Gaussian distributions representing the landmarks (resembling border-related cell recordings when plotted), with standard deviations corresponding to sensory uncertainty (noise in the sensory model). Such grids can easily be learned and provide some robustness to sensory and motor uncertainty. Note that since our emphasis here is on localization, the representation mechanism of landmarks is unimportant [9].

Similarly to motion commands, sensory information is also composed of a linear and angular component (range and bearing to a landmark), and also contains added Gaussian noise. Specifically, at each time step the agent receives N measurements m'_j, where

$$m'_j = m_j + \mathcal{N}(1, R), \text{ where } j = 1, \cdots, N \text{ and } R = \begin{bmatrix} \sigma_r^2 & 0 \\ 0 & \sigma_b^2 \end{bmatrix},$$

[8] Although drawing with replacement seems to arrive at more accurate and lower uncertainty estimates in less time steps, which is the reason that this approach is prevalent in robotics. We have sacrificed some performance for plausibility, without altering the underlying principle.

[9] We have also compared the agent's behaviour when using a fixed, pre-defined map in the its memory, which has yielded similar results but somewhat less uncertainty.

and σ_r^2 and σ_b^2 are the variance parameters controlling the amount of noise added to the range and bearing information. The only parameters we have adjusted to fit the model to the data in the Results section were these mentioned noise variance parameters for the motion model and the sensory model $(\sigma_v^2, \sigma_\omega^2, \sigma_r^2, \sigma_b^2)$, and the numbers of particles used and discarded.

The agent does not have an action selection mechanism; it executes a pre-defined control sequence designed to match the experimental conditions in the replicated experiments as closely as possible, including movement speed and observed trajectory. The 2D environment was also designed to match the environment used in the experiments, including landmark configurations and distances and agent starting point. The agent executes the pre-defined action sequence, receives sensory information according to the sensor model, estimates its location with the particle filtering approach described above, and uses the sensory information within the described Bayesian approximation to correct accumulating path integration errors. This algorithm can be summarized by the following simplified pseudocode:

```
//loop through pre-defined motor commands

for motorcommand_i in controlsequence
  timestep++

  //update particles
  for particle_i in particles
    //update particle_i using the motion model
    particle_i.setState(motionModel(particle_i.location, motorcommand_i))

    //set weight according to sensor model
    particle_i.setWeight(measurementProbability(currentMeasurement))
  end
  bestGuessLocation = mean(particle_i.location)

  //discard and replace M 'weak' particles
  m=0
  while m<M
    draw i with probability ~(1-particle_i.weight)
    particle_i = new particle from motionModel(bestGuessLocation, motorcommand_i)
  end

  //update environment representation
  updateMap(currentMeasurements)
end
```

The standard deviation of the particle set was recorded at each time step and for each condition, and used as a measure of 'uncertainty' in the graphs in the Results section.

Acknowledgments

The authors gratefully acknowledge the infrastructure provided by the University of Manchester, which has made this research possible; thought-provoking personal communications with many members of the Cognitive Computing Research Group at the University of Memphis; and the helpful comments of Steve Strain, who has read and commented on the manuscript.

References

1. Knill DC, Pouget A (2004) The Bayesian brain: the role of uncertainty in neural coding and computation. Trends in Neurosciences 27: 712–9.

2. O'Keefe J, Dostrovsky J (1971) The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. Brain Research 34: 171–175.

3. Burgess N (2008) Spatial cognition and the brain. Annals of the New York Academy of Sciences 1124: 77–97.

4. McNaughton BL, Battaglia FP, Jensen O, Moser EI, Moser MB (2006) Path integration and the neural basis of the 'cognitive map'. Nature Reviews Neuroscience 7: 663–78.

5. Moser EI, Kropff E, Moser MB (2008) Place cells, grid cells, and the brain's spatial representation system. Annual Review of Neuroscience 31: 69–89.

6. Zilli Ea (2012) Models of Grid Cell Spatial Firing Published 2005 - 2011. Frontiers in Neural Circuits 6: 1–17.

7. Etienne AS, Maurer R, Sguinot V (1996) Path integration in mammals and its interaction with visual landmarks. Journal of Experimental Biology 199: 201-9.

8. Jeffery KJ (2007) Self-localization and the entorhinal-hippocampal system. Current Opinion in Neurobiology 17: 684–91.

9. Kloosterman F, Van Haeften T, Witter MP, Lopes da Silva FH (2003) Electrophysiological characterization of interlaminar entorhinal connections: an essential link for re-entrance in the hippocampalentorhinal system. European Journal of Neuroscience 18: 3037–3052.

10. Tcheang L, Bülthoff HH, Burgess N (2011) Visual influence on path integration in darkness indicates a multimodal representation of large-scale space. Proceedings of the National Academy of Sciences of the United States of America 108: 1152–7.

11. Pilly PK, Grossberg S (2012) How do spatial learning and memory occur in the brain? Coordinated learning of entorhinal grid cells and hippocampal place cells. Journal of Cognitive Neuroscience 24: 1031–54.

12. Samu D, Eros P, Ujfalussy B, Kiss T (2009) Robust path integration in the entorhinal grid cell system with hippocampal feed-back. Biological Cybernetics 101: 19–34.

13. Fox CW, Prescott TJ (2010) Hippocampus as unitary coherent particle filter. In: IJCNN. IEEE Press, pp. 1-8.

14. Denève S, Duhamel JR, Pouget A (2007) Optimal sensorimotor integration in recurrent cortical networks: a neural implementation of Kalman filters. The Journal of neuroscience : the official journal of the Society for Neuroscience 27: 5744–56.

15. Pfuhl G, Tjelmeland H, Biegler R (2011) Precision and reliability in animal navigation. Bulletin of Mathematical Biology 73: 951–77.

16. Paulin MG, Hoffman LF (2011) Bayesian head state prediction: Computing the dynamic prior with spiking neurons. 2011 Seventh International Conference on Natural Computation : 445–449.

17. Wilson RC, Finkel LH (2009) A neural implementation of the kalman filter. In: Advances in Neural Information Processing Systems 22. pp. 2062–2070.

18. MacNeilage PR, Ganesan N, Angelaki DE (2008) Computational approaches to spatial orientation: from transfer functions to dynamic Bayesian inference. Journal of Neurophysiology 100: 2981–96.

19. Durrant-Whyte H, Bailey T (2006) Simultaneous localization and mapping: Part 1. Robotics Automation Magazine, IEEE 13: 99 -110.

20. Solstad T, Boccara CN, Kropff E, Moser MB, Moser EI (2008) Representation of geometric borders in the entorhinal cortex. Science 322: 1865–8.

21. Taube JS (2007) The head direction signal: origins and sensory-motor integration. Annual Review of Neuroscience 30: 181–207.

22. Lever C, Burton S, Jeewajee A, O Keefe J, Burgess N (2009) Boundary vector cells in the subiculum of the hippocampal formation. Journal of Neuroscience 29: 9771–7.

23. Barry C, Lever C, Hayman R, Hartley T, Burton S, et al. (2006) The boundary vector cell model of place cell firing and spatial memory. Reviews in the Neurosciences 17: 71–97.

24. Shinder ME, Taube JS (2010) Differentiating ascending vestibular pathways to the cortex involved in spatial cognition. Journal of Vestibular Research : Equilibrium & Orientation 20: 3–23.

25. Hafting T, Fyhn M, Molden S, Moser MB, Moser EI (2003) Microstructure of a spatial map in the entorhinal cortex. Nature 436: 801–806.

26. O'Keefe J, Burgess N (2005) Dual phase and rate coding in hippocampal place cells: theoretical significance and relationship to entorhinal grid cells. Hippocampus 15: 853–866.

27. Doeller CF, Barry C, Burgess N (2011) From Cells to Systems: Grids and Boundaries in Spatial Memory. The Neuroscientist .

28. Doeller CF, Barry C, Burgess N (2010) Evidence for grid cells in a human memory network. Nature 463: 657–661.

29. Ekstrom AD, Kahana MJ, Caplan JB, Fields TA, Isham EA, et al. (2003) Cellular networks underlying human spatial navigation. Nature 424: 184-187.

30. Solstad T, Moser EI, Einevoll GT (2006) From grid cells to place cells : A mathematical model. Hippocampus 1031: 1026–1031.

31. Baumann O, Mattingley JB (2010) Medial parietal cortex encodes perceived heading direction in humans. Journal of Neuroscience 30: 12897–12901.

32. Redgrave P (2007) Basal ganglia. Scholarpedia 2: 1825.

33. Marlinski V, McCrea RA (2009) Self-motion signals in vestibular nuclei neurons projecting to the thalamus in the alert squirrel monkey. Journal of Neurophysiology 101: 1730–1741.

34. Lopez C, Blanke O (2011) The thalamocortical vestibular system in animals and humans. Brain Research Reviews 67: 119–146.

35. Fetsch CR, Wang ST, Gu Y, DeAngelis GC, Angelaki DE (2007) Spatial reference frames of visual, vestibular, and multimodal heading signals in the dorsal subdivision of the medial superior temporal area. Journal of Neuroscience 27: 700–712.

36. Squire LR, Stark CEL, Clark RE (2004) The medial temporal lobe. Annual Review of Neuroscience 27: 279–306.

37. Eichenbaum H, Fortin NJ (2009) The neurobiology of memory based predictions. Philosophical transactions of the Royal Society of London Series B, Biological sciences 364: 1183–91.

38. Lisman J, Redish AD (2009) Prediction, sequences and the hippocampus. Philosophical transactions of the Royal Society of London Series B, Biological Sciences 364: 1193–201.

39. Bird CM, Burgess N (2008) The hippocampus and memory: insights from spatial processing. Nature reviews Neuroscience 9: 182–94.

40. Lee SA, Sovrano Va, Spelke ES (2012) Navigation as a source of geometric knowledge: Young children's use of length, angle, distance, and direction in a reorientation task. Cognition 123: 144–61.

41. Smith RC, Park M, Cheeseman P (1986) On the Representation and Estimation of Spatial Uncertainty. The International Journal of Robotics Research 4: 56-68.

42. Thrun S, Burgard W, Fox D (2005) Probabilistic Robotics (Intelligent Robotics and Autonomous Agents series). Intelligent robotics and autonomous agents. The MIT Press.

43. Ernst MO, Banks MS (2002) Humans integrate visual and haptic information in a statistically optimal fashion. Nature 415: 429–33.

44. Krding KP, Ku Sp, Wolpert DM (2004) Bayesian integration in force estimation. Journal of Neurophysiology 92: 3161-3165.

45. Krding KP, Wolpert DM (2006) Bayesian decision theory in sensorimotor control. Trends in Cognitive Sciences 10: 319 - 326.

46. Cheng K, Shettleworth SJ, Huttenlocher J, Rieser JJ (2007) Bayesian integration of spatial information. Psychological Bulletin 133: 625–37.

47. Kersten D, Schrater P (2005) Pattern Inference Theory: A Probabilistic Approach, John Wiley & Sons, Ltd. pp. 191–228. doi:10.1002/0470013427.ch7. URL http://dx.doi.org/10.1002/0470013427.ch7.

48. Derdikman D (2009) Are the boundary-related cells in the subiculum boundary-vector cells? The Journal of Neuroscience 29: 13429–31.

49. Hangya B, Li Y, Muller RU, Czurk A (2010) Complementary spatial firing in place cellinterneuron pairs. The Journal of Physiology 588: 4165–4175.

50. Gloveli T (2010) Hippocampal spatial navigation: interneurons take responsibility. The Journal of Physiology 588: 4609-4610.

51. O'Keefe J (1976) Place units in the hippocampus of the freely moving rat. Experimental Neurology 51: 78–109.

52. Ma WJ, Beck JM, Latham PE, Pouget A (2006) Bayesian inference with probabilistic population codes. Nature Neuroscience 9: 1432–1438.

53. Ma WJ, Beck JM, Pouget A (2008) Spiking networks for Bayesian inference and choice. Current Opinion in Neurobiology 18: 217–22.

54. Friston K (2009) The free-energy principle: a rough guide to the brain? Trends in Cognitive Sciences 13: 293–301.

55. Vilares I, Kording K (2011) Bayesian models: the structure of the world, uncertainty, behavior, and the brain. Annals of the New York Academy of Sciences 1224: 22–39.

56. Harrison LM, Duggins A, Friston KJ (2006) Encoding uncertainty in the hippocampus. Neural Networks 19: 535–546.

57. Vanni-Mercier G, Mauguière F, Isnard J, Dreher JC (2009) The hippocampus codes the uncertainty of cue-outcome associations: an intracranial electrophysiological study in humans. The Journal of Neuroscience 29: 5287–94.

58. Mathys C, Daunizeau J, Friston KJ, Stephan KE (2011) A bayesian foundation for individual learning under uncertainty. Frontiers in Human Neuroscience 5: 39.

59. Lengyel M, Dayan P (2007) Uncertainty, phase and oscillatory hippocampal recall. In: 19th Neural Information Processing Systems Conference (NIPS 2006). MIT Press, pp. 833 - 840.

60. OKeefe J, Burgess N (1996) Geometric determinants of the place fields of hippocampal neurons. Nature 381: 425–428.

61. Muller RU, Kubie JL, Ranck JB (1987) Spatial firing patterns of hippocampal complex-spike cells in a fixed environment. Journal of Neuroscience 7: 1935–1950.

62. Van Cauter T, Poucet B, Save E (2008) Unstable ca1 place cell representation in rats with entorhinal cortex lesions. European Journal of Neuroscience 27: 1933–1946.

63. Allen K, Fuchs EC, Jaschonek H, Bannerman DM, Monyer H (2011) Gap junctions between interneurons are required for normal spatial coding in the hippocampus and short-term spatial memory. The Journal of Neuroscience 31: 6542-6552.

64. Capogna M (2011) Neurogliaform cells and other interneurons of stratum lacunosum-moleculare gate entorhinal-hippocampal dialogue. The Journal of Physiology 589: 1875-1883.

65. Hartley T, Burgess N, Lever C, Cacucci F, O'Keefe J (2000) Modeling place fields in terms of the cortical inputs to the hippocampus. Hippocampus 10: 369–79.

66. Hartley T, Trinkler I, Burgess N (2004) Geometric determinants of human spatial memory. Cognition 94: 39–75.

67. Burwell R, Hafeman D (2003) Positional firing properties of postrhinal cortex neurons. Neuroscience 119: 577 - 588.

68. Czurko A, Hirase H, Csicsvari J, Buzsaki G (1999) Sustained activation of hippocampal pyramidal cells by "space clamping" in a running wheel. European Journal of Neuroscience 11: 344–352.

69. Maurer AP, Vanrhoads SR, Sutherland GR, Lipa P, McNaughton BL (2005) Self-motion and the origin of differential spatial scaling along the septo-temporal axis of the hippocampus. Hippocampus 15: 841–52.

70. Terrazas A, Krause M, Lipa P, Gothard KM, Barnes Ca, et al. (2005) Self-motion and the hippocampal spatial metric. The Journal of Neuroscience 25: 8085–96.

71. Chen Z, Resnik E, McFarland JM, Sakmann B, Mehta MR (2011) Speed controls the amplitude and timing of the hippocampal gamma rhythm. PloS ONE 6: e21408.

72. Park E, Dvorak D, Fenton AA (2011) Ensemble place codes in hippocampus: Ca1, ca3, and dentate gyrus place cells have multiple place fields in large environments. PLoS ONE 6: e22349.

73. Leutgeb S, Leutgeb JK, Treves A, Moser MB, Moser EI (2004) Distinct ensemble codes in hippocampal areas ca3 and ca1. Science 305: 1295-1298.

74. Lisman JE, Otmakhova NA (2001) Storage, recall, and novelty detection of sequences by the hippocampus: elaborating on the socratic model to account for normal and aberrant effects of dopamine. Hippocampus 11: 551–568.

75. Fyhn M, Hafting T, Treves A, Moser MB, Moser EI (2007) Hippocampal remapping and grid realignment in entorhinal cortex. Nature 446: 190–4.

76. Derdikman D, Moser EI (2010) A manifold of spatial maps in the brain. Trends in Cognitive Sciences 14: 561–9.

77. Kjelstrup KB, Solstad T, Brun VH, Hafting T, Leutgeb S, et al. (2008) Finite scale of spatial representation in the hippocampus. Science (New York, NY) 321: 140–3.

78. Brun VH, Solstad T, Kjelstrup KB, Fyhn M, Witter MP, et al. (2008) Progressive increase in grid scale from dorsal to ventral medial entorhinal cortex. Hippocampus 18: 1200–1212.

79. Csicsvari J, Hirase H, Mamiya A, Buzsáki G (2000) Ensemble patterns of hippocampal CA3-CA1 neurons during sharp wave-associated population events. Neuron 28: 585–594.

80. Philbeck JW, Behrmann M, Levy L, Potolicchio SJ, Caputy AJ (2004) Path integration deficits during linear locomotion after human medial temporal lobectomy. Journal of Cognitive Neuroscience 16: 510–520.

81. Gerstner W, Kistler W (2002) Spiking Neuron Models: An Introduction. New York, NY, USA: Cambridge University Press.

82. Burke SN, Maurer AP, Nematollahi S, Uprety AR, Wallace JL, et al. (2011) The influence of objects on place field expression and size in distal hippocampal ca1. Hippocampus 21: 783–801.

83. Longtin A (2011) Neuronal noise. Scholarpedia .

84. Nardini M, Jones P, Bedford R, Braddick O (2008) Development of cue integration in human navigation. Current Biology 18: 689–93.

85. Lisman, John (1999) Relating hippocampal circuitry to function: recall of memory sequences by reciprocal dentate-CA3 interactions. Neuron 22(2): 233–42.

86. McNaughton BL, Barnes CA, Gerrard JL, Gothard K, Jung MW, et al. (1996) Deciphering the hippocampal polyglot: the hippocampus as a path integration system. Journal of Experimental Biology 199: 173–185.

87. Joseph D Monaco JJK, Zhang K (2011) Sensory feedback, error correction, and remapping in a multiple oscillator model of place cell activity. Frontiers in Computational Neuroscience 5.

88. Maloney LT, Mamassian P (2009) Bayesian decision theory as a model of human visual perception: Testing bayesian transfer. Visual Neuroscience 26: 147-155.

89. Colombo M, Series P (2012) Bayes in the Brain–On Bayesian Modelling in Neuroscience. The British Journal for the Philosophy of Science .

90. Britten K, Shadlen M, Newsome W, Movshon J (1992) The analysis of visual motion: a comparison of neuronal and psychophysical performance. The Journal of Neuroscience 12: 4745-4765.

91. Shadlen M, Britten K, Newsome W, Movshon J (1996) A computational analysis of the relationship between neuronal and behavioral responses to visual motion. The Journal of Neuroscience 16: 1486-1510.

92. Stocker AA, Simoncelli EP (2006) Noise characteristics and prior expectations in human visual speed perception. Nature Neuroscience 9: 578–585.

93. Deneve S, Latham PE, Pouget A (1999) Reading population codes: a neural implementation of ideal observers. Nature Neuroscience 2: 740–745.

94. Anastasio TJ, Patton PE, Belkacem-Boussaid K (2000) Using bayes rule to model multisensory enhancement in the superior colliculus. Neural Computation 12: 1165–1187.

95. Beck JM, Ma WJ, Kiani R, Hanks T, Churchland AK, et al. (2008) Probabilistic population codes for bayesian decision making. Neuron 60: 1142 - 1152.

96. Montemerlo M, Thrun S (2007) FastSLAM: A Scalable Method for the Simultaneous Localization and Mapping Problem in Robotics (Springer Tracts in Advanced Robotics). Secaucus, NJ, USA: Springer-Verlag New York, Inc.

97. Caesarendra W, Niu G, Yang BS (2010) Machine condition prognosis based on sequential monte carlo method. Expert Systems with Applications 37: 2412–2420.

98. Elfes A (1989) Using occupancy grids for mobile robot perception and navigation. Computer : 57.

Figure Legends

Tables