

Learning from Nature: Biologically Inspired Robot Navigation and SLAM—A Review

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Abstract In this paper we summarize the most important neuronal fundamentals of navigation in rodents, primates and humans. We review a number of brain cells that are involved in spatial navigation and their properties. Furthermore, we review RatSLAM, a working SLAM system that is partially inspired by neuronal mechanisms underlying mammalian spatial navigation.

Keywords Biologically inspired robotics · SLAM

1 Introduction

The SLAM problem has been on the agenda of countless robotics researchers during the last two decades. A huge variety of algorithms has been developed over the years, since the term first appeared in 1986. Today, probabilistic approaches clearly dominate the field. In this paper, we do not want to review these many algorithms or the required mathematical background yet again. Instead, we want to direct the reader's attention towards intelligent systems that solve the localization and mapping problem on an everyday basis, without ever being acknowledged for it: We ourselves, humans and the many animals that move effortlessly through their environment, finding their ways inside their familiar realms, beyond, and back.

Since we have only very limited space available for our review, we decided to focus on the neuronal fundamentals

of navigation, especially on a number of brain cells that are involved in spatial navigation in rodents, primates and humans. We want to shortly review their astonishing properties that may not be known to all researchers working in the field of robotics or SLAM, but may provide valuable inspiration for future work and developments in the SLAM and robotics community. The second part of the paper reviews a working SLAM system that was partially inspired by these brain mechanisms and has recently performed well in a very large SLAM challenge, successfully mapping 66 km of urban roads.

2 Neuronal Fundamentals of Rodent and Primate Navigation

During the past decades, but also very recently, a variety of cell types have been identified in certain areas of the mammalian brain that seem to be involved in spatial navigation. Experimental results indicate several cell types that represent position, orientation, complete pose, or the proximity of spatial boundaries. Other structures in the brain seem to be able to perform dead reckoning, or recognize places by their visual appearance. The knowledge in the field stems mainly from experiments with rodents like rats, supposedly for practical reasons. Results from experiments with primates or humans are rare, but support the findings from rodents, suggesting that primate and human navigation adheres to the same principles as rodent navigation.

The first reports of brain structures supporting spatial navigation reach back to the 1970's. However, the very recent discovery of two complete new types of cells in 2005 and late 2008 indicates how incomplete our knowledge of this field is.

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This first part of the paper reviews the cell assemblies in rodent and primate brains that seem to be important for spatial navigation. We also review their most important properties in a very condensed way. We refer the reader to the original literature for more comprehensive information.

2.1 Place Cells

In 1971 John O'Keefe and Jonathan Dostrovsky reported their results from experiments with rats that revealed the existence of special cells in the rats brains that responded to "places" [29]. For the experiments the rats had electrodes fixed to their skulls and descended into their brains. Apart from that, the rats could move around freely while the electrodes constantly recorded the activity of nearby cells in the hippocampus region of the brain. The special *place cells* that O'Keefe and Dostrovsky reported, showed a remarkable characteristic: While being inactive most of the time, they suddenly start to fire whenever the rat enters a certain area in the environment, the so called *place field* of that cell.

These place fields differ in size and shape. In a later paper, O'Keefe reported varying sizes between 10 cm² and "almost half the total area of the maze" [27]. The maze in this experiment was T-shaped, with a circular platform (diameter 35 cm) at the junction of the three arms (each 38 cm × 15 cm).

The place fields of several place cells overlap, so that several place cells will be active at a given moment. However, the spikes they generate will usually not occur all at the same time. The temporal pattern (i.e. the exact moments when each of the active place cells fires) depends on the position of the rat inside the individual place fields. This mechanism, called *phase precession* was first reported by O'Keefe and Recce [31] and later confirmed by Skaggs et al. [41]. This temporal firing pattern may help to refine the position: The place cells do not merely indicate that the rat is *somewhere* inside the cell's place field, but their temporal firing characteristics may also encode the position inside that place field.

The place cell activity is driven by visual cues (or "landmarks"), i.e. the rat is able to recognize places in the environment by visual information. Several experiments proved that the place fields could be moved or otherwise influenced by moving visual landmarks (e.g. [28, 32]). However, even in complete darkness or after the visual landmarks were removed, the activity patterns in the place cells keep changing when the rat is moving. Place cells are still able to represent and update the animal's position in a known environment even when no landmarks are visible anymore [26]. This strongly indicates that self-motion cues are used to perform *path integration*, which corresponds to dead reckoning in the SLAM-context. However, exactly how this path integration is performed, has yet to be determined. It seems that the hippocampus, the region where the place cells are

located, can not perform this task on its own. Other systems outside the hippocampus seem to be involved, supposedly also the *grid cells* that are described next [25].

Place cells were first discovered in rats in 1971 [29] but have more recently been reported in primates [17] (1999) and may also be present in the human hippocampus [10] (2003).

2.2 Grid Cells

After their discovery, place cells were thought to be the key elements of neuronal representation of space and navigation, forming a so called *cognitive map* [30]. However, lesion studies suggested another type of cells supporting navigation to be located in the *entorhinal cortex*, a brain region with strong connections to the areas in the hippocampus where the place cells were found [24]. Fyhn et al. found these postulated entorhinal cell assemblies in rats (up to now no evidence of them has been found in primates or humans) and published their findings in 2004 [13]. The activity of these newly discovered cells was modulated by the position of the animal, similar to the already known place cells.

Further experiments by Hafting et al. [15] in larger environments revealed an impressive property of these new cells: Unlike place cells, they fire at multiple locations in space. These locations form a regular tessellating pattern that covers the whole recorded environment. Because of the grid-like structure of the firing fields, the cells were coined *grid cells*.

Sargolini et al. [40] later reported the findings of so called conjunctive grid cells that showed direction tuning, i.e. grid cells that were sensitive to global orientation and fired only when the animal was facing a particular direction.

Similar to place cells, the firing fields of grid cells are influenced by visual landmarks, Hafting and colleagues [15] report the grid cells to be "anchored to external cues". This was verified by recording the grid cell activity from rats moving around freely in a circular box of 2 meters diameter. Visual landmarks (so called cue cards) were attached to the walls of this box, and the environment behind the box was concealed by curtains. When the visual landmarks were shifted (rotated) to other places on the circular wall, the grid fields rotated in a similar manner.

However, Hafting et al. also report that the grid-shaped firing fields were maintained without any visual cues, even in total darkness. Thus it seems that grid cells, just like place cells, receive and rely on self-motion information as well. Visual cues seem to be used to re-align the position represented in both cell types to the landmarks present in the environment [25].

2.3 Head Direction Cells

While place cells and grid cells provide the animal with a representation of its position in allocentric space, head di-

rection cells represent the global orientation of the animal's head. These cells, that were first found in rats by James B. Ranck, Jr. in 1984 and further examined by Jeffrey S. Taube in 1990 [45], are most active when the animal's head points into the cell's preferred direction. This preferred direction is aligned with an allocentric (global) coordinate frame. It is *not* influenced by the orientation of the body or the position of the animal in the environment. This way, head direction cells can be seen as an internal compass.

Besides the cells reported by Taube in 1990 [45], later studies showed that specialized cells are able to anticipate the future head direction based on angular velocity information [5]. Other cells showed a responsivity to the angular velocity of the animal's head [18].

Just like place cells and grid cells, the activity of head direction cells is driven both by visual cues and ego-motion signals. The animal is able to maintain and update the activity in its head direction cells even when moving around in darkness, although without being reset by visual landmarks, the head direction represented by the cells begins to drift [37].

Head direction cells are not only found in rodents, but have been reported in primates as well [34, 37]. In rodents, they seem to influence some grid cells, leading to the so called conjunctive grid cells reported by Sargolini et al. [40] that showed both place and orientation tuning.

2.4 Spatial View Cells

The place cells described above provide rodents and supposedly also primates and humans with a mechanism to represent their position in allocentric space. In addition to place cells, Rolls and O'Mara reported a type of cell in the primate hippocampus that could not be found in rodents: *spatial view cells* [36–38]. These cells fire whenever the animal is looking at particular cues or landmarks in the environment, independent of the current position. They do not fire when the animal *is* at a certain place (like place cells do) but rather when the animal *looks* at a certain place. The different behavior of the two cell types was later explained by de Araujo et al. [8] to be caused by different sizes of the visual receptive fields. According to this explanation, rodents have a much wider field of view compared to primates (270° vs. 30°). De Araujo provided a computational model that demonstrated the formation of place cells and spatial view cells through a learning process dependent on the visual stimuli.

Robertson et al. [35] reported that at least some spatial view cells retain their spatial characteristics in known environments even when the original landmarks could not be seen anymore.

2.5 Place-by-Direction and Border Cells

In 2004 Cacucci et al. [7] reported the findings of cells in rats that combined the properties of place and head direction cells. Their so called *theta modulated place-by-direction cells* fire only when the animal is at a particular place, facing a particular direction. Thus these cells represent the complete 3 dimensional pose $(x, y, \theta)^T$ of the animal in a planar environment.

The most recently discovered type of cells that seem to be involved in navigation and the representation of the spatial structure of the environment was published in late 2008. The same group that reported the first findings of grid cells did now reveal the existence of cells that encode the animal's distance from geometric borders in the environment [42]. These cells fire when the animal is within a certain vicinity of an obstacle.

2.6 Summary

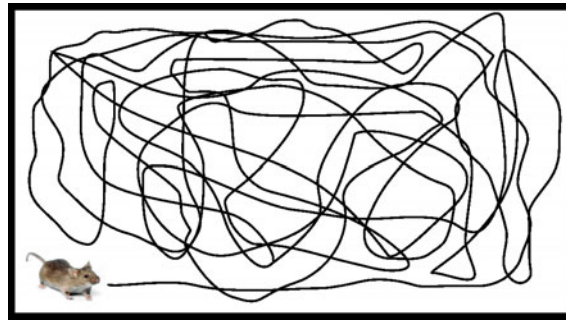
As we have seen, a number of different cell types that are involved in spatial navigation tasks have been proven to exist in different parts of the mammalian brain. Although by far the most experimental results stem from rats, experimental evidence for the existence of these cells in primates and humans have been reported, too. Figure 1 summarizes the most important properties of the different types of cells and sketches their firing patterns.

The experimental findings from several studies cited above reveal that at least place cells, grid cells and head direction cells are driven by both visual stimuli and self-motion cues: Their activity patterns are updated even when no visual stimuli (e.g. recognizable landmarks) are visible. However, visual information seem to dominate the self-motion cues: For example landmarks seem to be used to reset or realign the firing fields of different cell types.

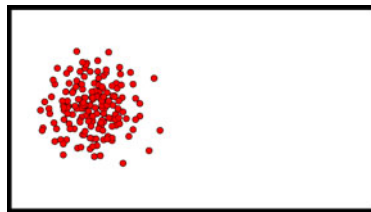
Expressing this in the usual terms of probabilistic filtering and SLAM, the self-motion cues (provided by the visual and vestibular system and proprioceptive stimuli) provide the control inputs u_t that are used to predict the system state \bar{x}_t (position and gaze direction). Visual cues form the measurement z_t and are used for a correction and update of the initial prediction to gain the resulting system state x_t . The belief distribution $\text{bel}(x_t)$ can be understood to be represented by the activity patterns of the different involved cell types.

Foo et al. [11, 12] conducted a series of experiments in order to determine how important visual landmarks are to human navigation performance. The human participants of the experiments could move around freely in a room of 12×12 meters while wearing a head-mounted display that provided visual input from a virtual reality world. The experiments showed that although humans are generally able

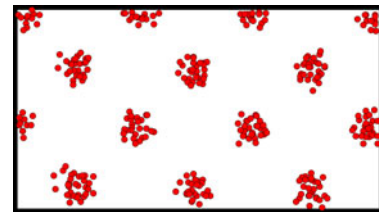
Fig. 1 Different cell types in mammalian brains that are involved in spatial navigation. The images illustrate how one single cell of a specific type fires depending on where a rat moving through a rectangular enclosed environment is located and oriented



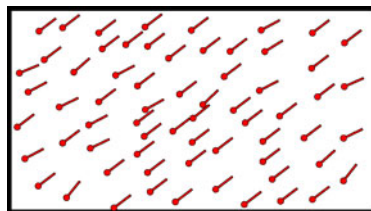
(a) A rat moving randomly in a rectangular enclosed environment. The following images show how one single cell of a specific type fires depending on where the rat is or how it is oriented.



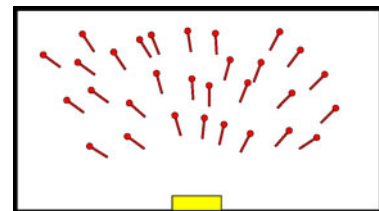
(b) A place cell fires when the animal is in a certain area of the environment. It represents the animal's position in global coordinates.



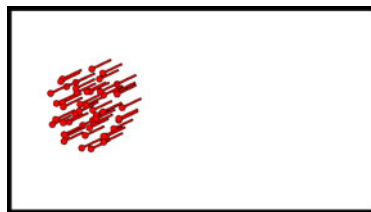
(c) A grid cell has multiple firing locations that form a grid covering the whole environment.



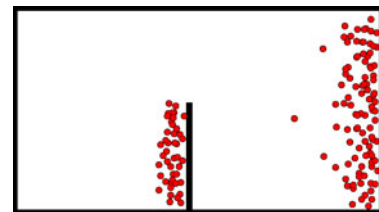
(d) A head direction cell fires whenever the animal looks into a certain direction. These cells perform like an internal compass.



(e) A spatial view cell fires whenever the animal looks at a certain landmark, independent on where in the environment the animal is located.



(f) A place-by-direction cell combines the properties of place and head direction cells and fires whenever the animal is in a particular area and facing a certain direction.



(g) Border cells fire in the vicinity of obstacles.

to rely on path integration for walking towards and reaching a learned goal location with fairly sufficient accuracy, they cannot combine these information into a global, consistent and accurate cognitive map that would allow them to perform precise navigation. Instead, they are highly dependent on distinguishable landmarks. Other studies like Sturz et al. [44] support these findings.

3 RatSLAM—A Biologically Motivated SLAM System

Over the past years, many research groups and authors have developed computational models for the cells found to be involved in animal navigation. Due to space constraints we can merely mention a few of the models that simulate spatial navigation processes on a neurological basis: Important

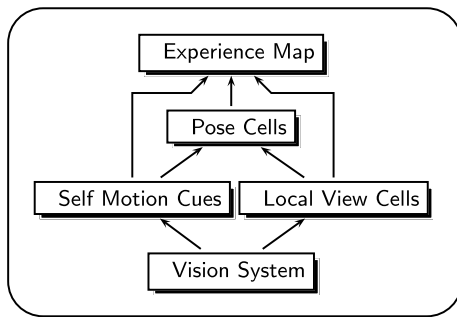


Fig. 2 The general structure of RatSLAM. The vision system provides the input for odometry information and place recognition. The pose cells are inspired by the rodent head direction and place cells, while the experience map is responsible for loop closing and maintaining a topologically consistent map

early work was done by Burgess et al. [6] and Redish and Touretzky [33]. Arleo et al. proposed influential ideas in several publications [1–3] that were later extended by Strösslín et al. [43] and Barrera and Weitzenfeld [4].

The work and the models mentioned above were strongly motivated by the underlying biological principles. Although some of them have been tested on real hardware like Khepera or Sony Aibo robots, none of the authors aimed at implementing a working large-scale SLAM algorithm. The goal was rather to verify the current understanding of neural principles underlying biological navigation. Therefore, the mentioned authors and their work are much closer to the fields of neuroscience or computational biology than to robotics.

RatSLAM, however, differs substantially in that point. Instead of trying to mimic its biological counterparts as closely as possible, the system borrows the important key ideas and adopts and simplifies them in order to gain computational feasibility. Despite these simplifications, it performs so well that it was recently [23] able to successfully map a 66 km long traverse of urban street networks, a challenge that is far from what other established SLAM methods have proven to master.

RatSLAM was first published by Milford and colleagues in 2003 [22] and gradually enhanced during the next years [19–21, 23]. Our description here concentrates on the latest implementation of the model as it was used in [23].

The general system architecture can be seen in Fig. 2. In its latest implementation, RatSLAM is a realtime vision only SLAM system. The vision module generates coarse estimates for forward velocity and rotation (self-motion cues) and scene descriptors that are used by so called *local view cells* to recognize already visited places during loop closure.

3.1 Pose Cells

The core of the system is a 3 dimensional *continuous attractor network* [39] of pose cells. Each cell in that network

represents a certain volume of space (e.g. $10\text{ m} \times 10\text{ m} \times 10^\circ$) and the combined activity pattern of all cells expresses the system's discretized belief of the robot's current pose. This mechanism bears resemblance to the histogram filter, a discretized version of the standard Bayes filter [46].

Each active cell in such an attractor network has an excitatory effect on it self and its close neighbors and an inhibitory effect on cells further away. This way, self-preserving packets of local activity form in the network. Due to the inhibition, these local packets compete, trying to annihilate one another until a stable state is reached. Each cell can receive additional stimuli from the local view cells which inject energy into the network. If the energy is injected close to an existing packet, that packet tends to move towards the injected energy. If it is injected further away and the injection continues over several network iterations, a new packet can eventually form, compete and finally supersede the old packet. The joint activity pattern of the whole network can be understood to be a discretized version of $\text{bel}(x_t)$, the belief distribution of the system state (robot pose) at time t . Note that the pose cell network is finite, but due to the mechanism that allows activity to wrap around the network borders it is not bounded. Hence the pose cell network is able to map the infinite space (x, y, θ) , although the mapping is in general ambiguous.

As in rodents and primates, self-motion cues (odometry) gradually update the pose hypotheses (path integration alias dead reckoning) while the robot moves around. In terms of probabilistic filtering, this is the prediction step. However, as pointed out explicitly by Milford and Wyeth [23], this path integration step does not introduce any growing uncertainty as would be the case in a truly probabilistic approach, because the activity patterns are merely shifted through the network but not altered in any other way.

Visual cues (recognition of visited places) are used to provide a global reference frame that corrects the path integration errors by injecting energy into the attractor networks as described above, which resembles the measurement update from Bayes filters. However, in the Bayes framework, the measurement update is done multiplicatively (by multiplying the predicted $\overline{\text{bel}}(x_t)$ and $p(z_t | x_t)$), whereas in RatSLAM it is done additively, as the local view cells add energy to the pose cells and can also strongly stimulate those pose cells that have not at all been activated during the prediction (path integration) step.

An important insight from early experiments [22] was that a stable pose estimate could not be maintained when position and orientation are represented in two different and independent network populations. A strong coupling between both hypotheses is necessary. This is achieved by the pose cell network that combines place cells and head direction cells and therefore resembles the combined place-by-direction cells mentioned in the first part.

3.2 The Experience Map

The experience map is responsible for managing a topologically and (to some extent) metrically consistent global map of the environment. It consists of single *experiences*, each bound to a particular position in space and connected to previous and successive other experiences. A new experience is created when the activity in the pose cells has been shifted a certain amount (due to self-motion cues), or when the scene descriptor from the vision system changed significantly, suggesting the robot entered a new “place”. This way, the experience map is a graph, where the experiences are the nodes and the connections between these experiences are the graph edges. These edges save odometry information that were measured by the vision system during the traversal from one experience to another.

Loop closure occurs when the robot revisits an already known area. The reactivated local view cell will trigger the corresponding node in the experience map and a new link between the last new entry and the reactivated old node will be formed. Due to the accumulated odometry errors, there will usually be a huge discrepancy between the expected position of the rediscovered node and the measured position according to the odometry information from the vision module. An algorithm similar to the graph relaxation [9] or spring-mass model [14] will distribute this error through the network and gradually restore topologic and metric integrity. In the end, the resulting map will be topologically correct and metrically sound. Unfortunately, Milford and Wyeth [23] did not provide any analysis on the metric accuracy of the generated maps compared to ground truth.

4 Conclusions

We shortly reviewed a number of different cells from the mammalian brain that are involved in spatial navigation. These cells have been verified to exist in rodents and partially also in primates and humans. During the past years different authors developed computational models for different sets of these cells and their interactions. Most of these models aim at verifying the understanding of the neurological mechanisms underlying navigation in rodents or primates.

RatSLAM is a working realtime vision-based SLAM system that incorporates important key ideas from biology. It differs from the established probabilistic approaches but has nonetheless been able to perform SLAM on a city-scale environment, successfully mapping 66 km of urban road network in realtime with a single camera as the only sensor.

In future work, a detailed analysis and comparison of results between RatSLAM and established probabilistic methods should be conducted on the same datasets in order to fully understand the differences and resemblances of both

worlds. As we mentioned above, the pose cell mechanism of RatSLAM appears to bear resemblances to the discretized versions of Bayes filters like Histogram filters. Future work should further investigate the consequences of the different strategies of measurement update (additive vs. multiplicative) and the influence of the pose cell system dynamics in depth. A more sophisticated yet biologically plausible vision system (e.g. based on attention modulation like [16]) could further improve the system’s performance. First preliminary experimental results by the authors support this hypothesis.

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