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Towards a Computational Theory of Rat Navigation

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A century of behavioral studies has generated an abundance of proposals for how animals represent and navigate through space. Recently, neurophysiological recording in freely-behaving animals has begun to reveal cellular correlates of these cognitive processes, such as the existence of place cells in hippocampus and head direction cells in postsubiculum and parietal cortex. We propose computational mechanisms to explain these phenomena.

A variety of computer models have demonstrated place cell-like responses, given inputs that encode distance and/or bearing to one or more landmarks. These models utilize machine learning algorithms such as competitive learning [Sharp 1991], recurrent backpropagation/Elman nets [Shapiro & Hetherington 1993, Hetherington & Shapiro 1993], genetic algorithms [Treves et al. 1992], competitive learning with radial basis units [Burgess et al. 1993], and specialized architectures employing a combination of delta rule and radial basis units [Schmajuk & Blair 1993].

The problem with all of these models is that their processing is mainly a function of visual input. The experimental literature clearly shows that hippocampal processing is not that simple. Specifically, although place fields *are* sensitive to visual input (they rotate in agreement with rotation of distal visual cues), place cells remain active when the lights are turned out, and place fields can form when the animal explores novel environments in the dark. Place cells also continue to fire when distal landmarks are removed, but permutation of landmarks causes the animal to behave as if it were in an unfamiliar environment. Finally, place cell firing may be dependent on head direction, at least under certain conditions. An acceptable model of place memory must allow the "current place" to be updated by non-visual means such as motor feedback, and must be both sensitive to visual cues and robust in their absence.

We propose a computational theory of the core of rat navigation abilities, based on coupled mechanisms for path integration, place recognition, and maintenance of head direction. We assume the rat has a path integration system (see [Etienne 1987, Mittelstaedt & Mittelstaedt 1980]) that is able to keep track of its current position relative to selected reference points. We postulate that hippocampal pyramidal cells form place descriptions by learning correlations between perceptual inputs and the rat's internal states, which include the output of the path integrator. Place codes are associated with landmark bearings, so that visual cues can recall previously stored directional information in a manner similar to McNaughton's local view hypothesis [McNaughton 1989].

We describe a connectionist implementation of this theory. Our model reproduces a variety of experimental observations, including reset of head direction in response to visual input, persistence of place fields in the absence of visual input, and modulation of place cell directional sensitivity. We compare our theory with other theories of hippocampal function and offer some predictions based on the model.

Behavioral and Biological Data

Place Cells

Over two decades ago, O'Keefe & Conway [1978] discovered pyramidal cells in the hippocampus that fire maximally when the rat occupies a particular location in the environment. They called these cells *place cells*. Numerous studies have since been performed to elucidate the characteristics of these cells [O'Keefe & Speakman 1987, Muller & Kubie 1987, McNaughton et al. 1989, Sharp et al. 1990, Quirk et al. 1990, Muller et al. 1991, Quirk et al. 1992].

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When a rat is deposited in a novel arena, place cells are rapidly recruited to code for locations in that environment [Quirk et al. 1990]. They develop a sensitivity to defining characteristics of the environment. In two visually similar but geometrically distinct arenas (one round and one rectangular), mostly disjoint sets of place cells are recruited [Muller & Kubie 1987]. Although each cell's place specificity is broadly tuned and varies depending on the available perceptual cues [Muller & Kubie 1987], their ensemble activity is sufficient to localize the rat's position to within a few centimeters [Wilson & McNaughton 1993]. Quantitative analysis further shows that when the animal is moving, the place code predicts its future position by about 120 milliseconds [Muller & Kubie 1989].

Once the rat has a notion of where it is, place cells continue to respond even when the lights are turned off [Quirk et al. 1990]. Most place cells also continue their activity when some of the visual cues are removed, although some fraction become inactive [O'Keefe & Conway 1978, O'Keefe & Speakman 1987, Markus et al. 1993]. This suggests that place cells are influenced by but not solely driven by visual input.

In open arenas, the most readily observable correlate to place cell activity is the rat's physical location. However, experimenters have observed activity being modulated by other aspects of behavior. For example, Eichenbaum [1987] reports correlates of hippocampal cell activity with task segments in an open arena where the rat is to repeat a sequence of actions: run to an odor-sampling port on one side of the room, discriminate the odor cue, and then, depending on the valence of the odor, run to the opposite side of the room to receive a reward. Some place cell responses were modulated by whether the rat was traveling to the odor port or the reward site as it crossed the place field.

Place cells are normally non-directional [Muller et al. 1991]. But in experiments where the rat is restricted to a corridor environment, such as an eight-arm maze, place cells readily become directionally tuned [McNaughton et al. 1989]. O'Keefe (personal communication) has observed that when rats are trained to run back and forth on a one dimensional track, place cells are initially non-directional, but after they become familiar with the task the cells develop directionality. However, when a food pellet is placed at the center of the track so the rat encounters it unexpectedly, there is preliminary indication that the ensuing arousal response is accompanied by place cells again becoming non-directional. This suggests that place fields may be modulated by attention.

McNaughton (personal communication) reports experiments by Gothard which begin with a rat performing a navigation task in a tightly controlled, cue-restricted environment where the primary visual cues are two cylinders. Additional, non-salient cues are gradually added until the environment is cue-rich. Place cells were observed to follow the position of the cylindrical landmarks (which can be moved about), ignoring the non-salient cues. This demonstrates that hippocampal place cells respond to a *cue set* that can be influenced by the animal's past experience.

Path Integration

Behavioral studies [Etienne 1987, Mittelstaedt & Mittelstaedt 1980] demonstrate that rats are able to wander randomly in the dark and then follow a direct path back to their starting point. They do so by integrating vestibular and kinesthetic cues along the path.

Although hippocampal lesions produce severe deficits in spatial tasks involving exteroceptive cues [O'Keefe & Nadel 1978], lesioned rats can continue to perform tasks that admit alternative strategies, such as path integration [Schacter & Nadel 1991]. For example, in a task where rats were passively transported from a reward site and then had to return without the use of visual or other cues, hippocampal lesions did not produce a deficit, whereas lesion of the caudate nucleus did [Abraham et al. 1983]. This suggests that the path integration system functions independently of the hippocampus.

Head direction

Taube et al. [1990a, 1990b] report cells in postsubiculum and related areas that fire maximally when the animal's head is facing in a particular direction. They are thus called *head direction cells*. The *preferred direction* for such a cell (i.e., the direction eliciting maximal response) is constant throughout an environment. In addition, the difference in preferred direction for any pair of cells is constant across all environments. But cells' preferred directions measured with respect to *true* North may differ across environments. Thus, the set of head direction cells in a rat defines a *directional framework* for each environment to which the animal is exposed.

Head direction cells continue to respond in the dark, but the animal's directional sense will eventually drift if no sensory input is available. In a familiar environment, if visual cues rotate while the rat is in the arena, preferred directions rotate by a corresponding amount. On the other hand, rotation of an unfamiliar environment does not change the head direction cells' preferred directions; the animal's vestibular sense, telling it that nothing has changed, overrides its visual experience (McNaughton, personal communication). When a rat has been disoriented by having been vigorously turned while blindfolded, upon re-entering a familiar environment with eyes uncovered, its cells sometimes revert back to their previously established preferred directions.

Thus, the rat learns a particular alignment of its directional framework with each environment. When disoriented, it restores this alignment by reference to visual landmarks.

A Computational Theory of Rat Navigation

Based on the above and other experimental observations, our theory of rat navigation postulates coupled mechanisms for path integration, place recognition, and maintenance of head direction, as shown in figure 1.

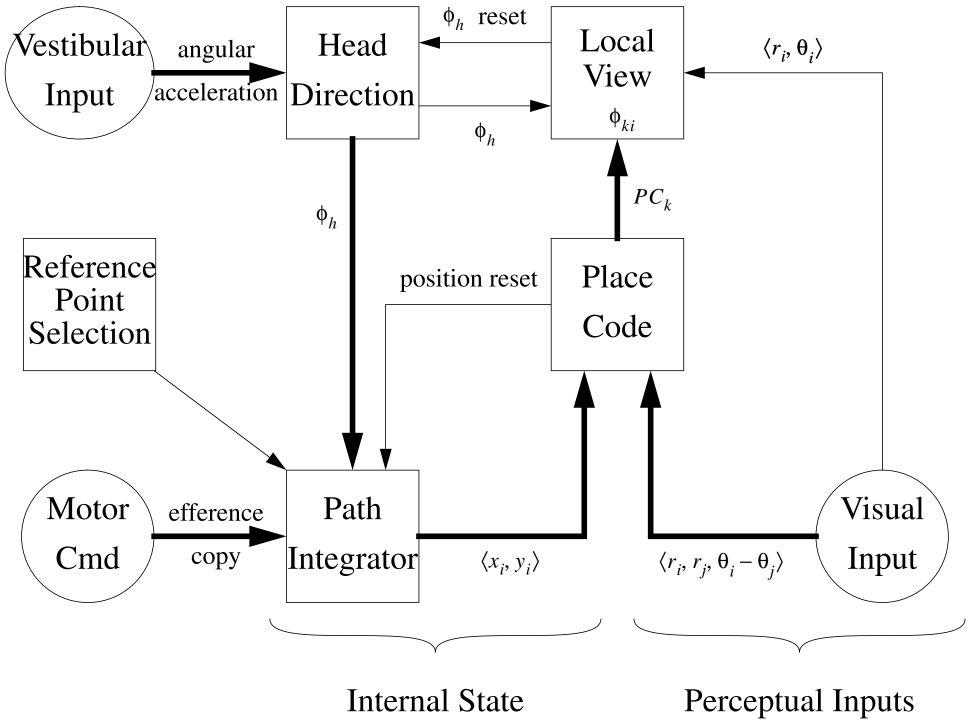

Figure 1: Suggested functional organization of orientation and recognition mechanisms in the rat. Circles are input quantities, boxes are computational modules; they do not necessarily correspond to disjoint or unique brain areas. Thick lines denote main information pathways.

Path integration and place recognition

As noted earlier, a variety of computer models have demonstrated responses similar to place cells. Because the focus of most of these models is on demonstrating formation of place fields from visual inputs, with a few exceptions [McNaughton et al. 1989, Hetherington & Shapiro 1993], none explain how place fields could remain when rats navigate in the dark.

In the model of Hetherington et al. [1993], an Elman net is trained with input sequences from paths to goal locations. This strengthens the recurrent connections between hidden units with nearby place fields. The appropriate place cell can then activate in sequence along paths to a goal without visual input. However, this scheme cannot account for acquisition and maintenance of place fields in the dark in tasks that do not have explicit goal locations [Quirk et al. 1990].

McNaughton et al. [1989] proposes that place cells associate motor actions with transitions between places, so that when visual inputs are unavailable, motor actions can drive the appropriate transitions in hippocampal activity. In effect, this proposes that hippocampus maintains its activity by performing path integration, but it can only do so for familiar regions of the environment. As discussed above, there is data suggesting that rats have a path integration module separate from hippocampus. It therefore seems more likely that efferents from the path integrator to hippocampus are responsible for place cell activity in the dark.

We hypothesize that the rat's path integration module maintains current position relative to a select set of *reference points* by integrating proprioceptive (vestibular) and kinesthetic (motor efference copy) cues. Reference points may be perceptually significant locations such as a corner of the room or a place with distinct odor or texture, but they might also be sensorily nondescript locations distinguished only by the past occurrence of some event, such as the spot in the arena where the rat was released to begin its first exposure to that environment.

The distinction between landmarks and reference points is important. Landmarks are distal cues that generate perceptual input, primarily bearing and distance information. Place cells learn to associate these cues with specific locations, so to be most useful, landmarks should be visible over a substantial portion of the environment. Reference points, on the other hand, are internally-defined locations tracked by the path integrator. They need not have any distinctive sensory attributes. In particular they do not need to be visible at a distance, as in the case of a nest site or burrow entrance.

A central claim of our theory is that the path integrator can maintain position simultaneously with respect to at least two reference points. The selection of "active" reference points is controlled by the animal's goals and attentional state. Place cells are associated with specific reference points, and so their activity is modulated by the active reference point set. Every time this set changes, such as when the animal turns around at the end of a corridor, one set of place cells becomes enabled while another set is disabled. The result is an apparent sensitivity of place cells to head direction. When arousal causes the animal to enlarge the active set to include reference points at both ends of the corridor, head direction sensitivity disappears.

Place recognition and head direction

McNaughton [1989] proposes that hippocampus encodes *local views* tuned to the perceptual features available at a location *with the head facing in a particular direction*. McNaughton et al. [1991] then describe a scheme where place cells encoding local-views are associated with the activity of head direction cells, so that when the rat is disoriented, head direction can be reset based on place cell activity.

We agree with the suggestion that place encodings should include landmark bearings to facilitate realignment of the head direction sense. However, place cells are mostly non-directional in open arenas [Muller et al. 1991]. We therefore think that place cell directional selectivity is unlikely to be the source of head direction realignment. Instead, we offer the following scheme for reconstructing head direction from nondirectional place cell activity.

Since place cells code for locations in a familiar environment, and the reference alignment of a familiar environment is fixed, a place cell activity pattern corresponds to a unique set of allocentric bearings to perceivable landmarks. We therefore suggest that as a rat familiarizes itself with the environment, it learns, in some area external to hippocampus, the correspondence between place codes and allocentric landmark bearings, which is equivalent to the "local view." Later, when the head direction sense is confused, the remembered allocentric bearings (retrieved via place cell activity) can be combined with egocentric bearings to reconstruct head direction. This retrieval process is shown schematically in figure 2.

While place cells are not tuned to allocentric bearings, they can use the differences in bearing between pairs of landmarks to localize points in space. This is because angular difference is constant regardless of head direction. Thus, animals can recognize locations based on landmark cues no matter what direction they are facing. In situations where place cells show directional selectivity [McNaughton et al. 1989], we suggest that the animal has limited its reference point set, e.g., it may only be tracking the reference point corresponding to the current goal location. Shifts in the choice of reference points when the animal reaches ends of corridor segments would result in place cells appearing directional.

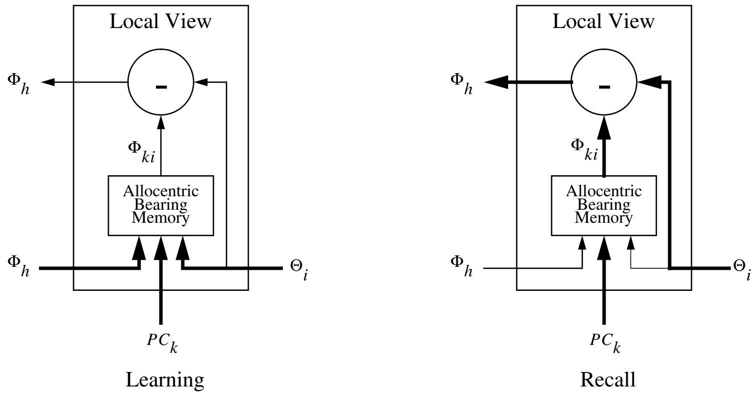

Figure 2: Computational structure of local view association. PC_k is activity of place cell k. Φ_h is head direction, and Θ_i is the current egocentric bearing of landmark i. Φ_{ki} is the allocentric bearing of landmark i at place k. During learning, PC_k is active and Φ_{ki} is recorded as $\Phi_h + \Theta_i$. To realign head direction, PC_k is used to recall Φ_{ki}, and Φ_h is computed as $\Phi_{ki} - \Theta_i$.

A Computer Model

Our place cells are radial basis units tuned to a conjunction of sensory and path integration inputs. Several units are recruited for each location in the environment. Each unit tunes itself to values present in the sensory and path integration systems for two landmarks and one reference point, chosen at random from the set available. The connectivity of these units is shown schematically in figure 3. Such use of radial basis units to model place cells is similar to those described in [Burgess et al. 1993, McNaughton et al. 1993]. In our current simulations, recruitment is done deterministically, but in principle it could be achieved using a Hebbian competitive network similar to those described in [Sharp 1991].

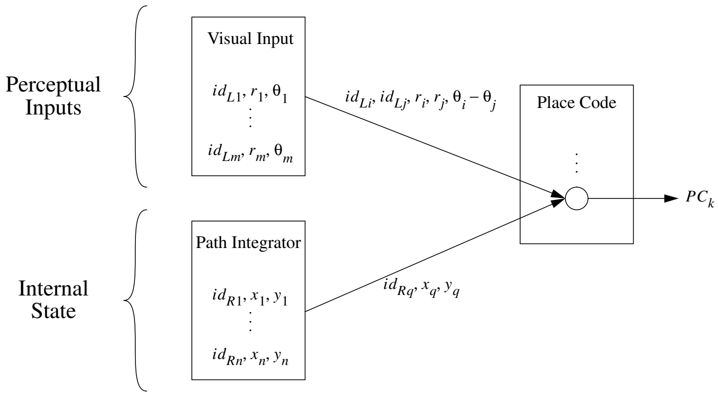

Figure 3: A modeled place cell is a radial-basis unit that tunes to the inputs at a particular location from two perceptual landmarks and one set of path integrator coordinates. id_L denotes an encoding of the identity of a visual landmark, r is the landmark's distance, and θ is its egocentric bearing. Similarly, id_R, x, and y are respectively the identity and Cartesian coordinates of a reference point.

Similar to the model in [Burgess et al. 1993] and unlike [McNaughton et al. 1993], we choose to combine sensory inputs from two landmarks rather than one. When the direction sense is lost, knowing distance to a single landmark only localizes position to a circle; using just egocentric bearing differences between two landmarks localizes to constant angle circular arcs [Levitt et al. 1987]; whereas distances to two landmarks localizes to two points. Thus, we use the combination of distances to and bearing differences between two identified landmarks to model localization to a unique location.

As discussed above, unlike previous computer models, we also include state information from the path integrator as part of the hippocampal input. The animal keeps track of its position in a set of Cartesian reference frames, each centered at an active reference point. For simplicity of exposition we align the x and y axes with East and North, respectively, when computing Cartesian coordinates. The reason for performing path integration in Cartesian rather than polar coordinates is computational stability, as discussed in [Gallistel 1990, p. 76].

The path integrator maintains position with respect to several reference points simultaneously. During exploration and learning, the maximum number of reference points may be active; each newly recruited unit would select one at random to tune to. When the environment has become familiar, a smaller number of reference points might be tracked, and position information is only available with respect to these active reference points. Thus, when a reference point is inactive, the place cells tuned to that point would be silent throughout the environment due to lack of appropriate input. An exception is that when the rat is disoriented, no information may be available from the path integrator, yet retrieval of an appropriate place code is needed. This is resolved by temporarily lowering place cells' dependence on the path integrator so that perceptual inputs alone can trigger place cell activity. In other situations, visual inputs may become unavailable. The dependence of place cells on input from the path integrator then needs to be increased. Mechanisms for such modulations on the extent in which the path integrator drive place cells are external to the present model.

In our simulation, we represent landmark and reference point identities by 1-of-n codes. Distances to landmarks use a distributed code implemented as of an array of radial basis units; differences in bearing are encoded similarly.

Results

Place cells associated with an active reference point are driven by a combination of path integrator and visual cues; they fire if the animal is within the cell's learned place field. For a wide range of parameter values, these cells produce place fields that are similar to those observed in real rats (see figure 4).

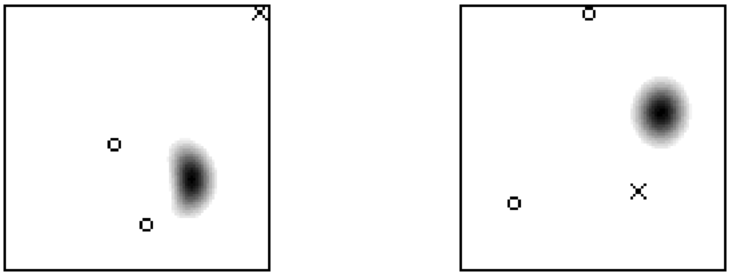

Figure 4: Receptive field of some simulated place cells. Each place cell tunes to a reference point denoted by an 'X' and two visual landmarks shown as circles.

If the rat is deposited in a random spot in the environment, the influence of the path integrator is momentarily reduced, and place units can be driven by visual inputs alone to determine the animal's present location. The path integrator could then be reset accordingly. When the lights are turned out, the path integrator continues to track the rat's position and trigger place cells. This qualitatively accounts for observations in [Quirk et al. 1990].

After disorientation, the animal needs to reestablish its head direction. Active place cell PC_k initiates recall of learned allocentric bearings Φ_{ki} for all visible landmarks i. The difference between Φ_{ki} and the current egocentric bearing Θ_i of the ith landmark gives the current head direction, Φ_h, as shown in figure 2. This reproduces the observations of Taube et al. [1990a, 1990b]

When only a few landmarks are removed, most radial basis place cells continue to receive input. For example, with eight landmarks there are 28 distinct pairings. Assume one place cell is allocated to each. When two landmarks are deleted, 15 of 28 cells continue to receive full input and are unaffected. One place cell receives no perceptual input while 12 cells receive input from one landmark instead of two. These cells can no longer localize positions based on perceptual inputs alone. But by also tuning to valid information from path integration, they could still maintain useful place fields. This is qualitatively similar to the experimental observations in [O'Keefe & Conway 1978, O'Keefe & Speakman 1987]. In contrast, a random transposition of all landmarks would cause most units recruited to code for the environment to become silent because most distances and differences in bearings would change. Other radial units might then be recruited to code for this new arrangement, as would be expected if the animal perceived the modified environment as novel. This would reflect the behavior observed in [Suzuki et al. 1980].

We simulate O'Keefe's one-dimensional track experiment using a reference point at each end of the track. Initially the animal maintains its position simultaneously with respect to both reference points, recruiting two sets of place cells to code for the environment. After becoming thoroughly familiar with the task, it only activates whichever reference point is ahead as it travels down the track. This externally provided attentional input to our model drives direction selectivity in the simulated place cells. Arousal in response to novelty (e.g., a food pellet encountered unexpectedly) results in simultaneous activation of both reference points and loss of direction sensitivity. A similar account can be given for the data in [Eichenbaum et al. 1987].

Discussion, future work, and predictions

As Gallistel points out [1990, p. 76], the accuracy of path integration is sensitive to the choice of representation. In polar coordinates, each update is dependent on the current position estimate, which magnifies cumulative errors. Cartesian systems do not have this problem, because calculation of Δx and Δy does not depend on x and y. We therefore model the states of the path integrator in a Cartesian representation. While the alignment of the Cartesian axes with North and East may seem arbitrary, the sinusoidal array [Touretzky et al. 1993], a spatially distributed phasor encoding, would be a plausible generalization.

In our simulations, the path integrator keeps track of the animal's current position. Instead, if it were to use the motor efference copy to anticipate the rat's position some 120 milliseconds in the future, the resulting place code would then predict the future position of the rat, as described in [Muller & Kubie 1989]. This would not be possible if place cells were driven by perceptual inputs alone.

Given two or more landmarks, a variety of combinations of distance and bearings can be used to localize points in space. For example, Sharp's model uses the conjunction of distances to multiple identified landmarks to reproduce place fields [Sharp 1991]. Similarly, Burgess et al. [1993] use distances to two landmarks.

Most models use fixed combinations of cues to determine location. However, we suggest that the information content in different cue types varies based on landmark properties. For example, while the estimate of distance to a landmark may be very precise when the landmark is nearby, the angles between landmarks can be more informative when the landmarks are farther away. The Hebbian rule has been shown to be closely related to an information maximization principle [Linsker 1987]. Hippocampal associative Hebbian synapses might perhaps be dynamically choosing those spatial primitives with the maximal information content.

We also believe this principle can be applied to the task of retrieving head direction based on perceptual input and place codes. First, to allow for Hebbian learning, the encoding used in the present model for allocentric bearings of landmarks would have to be changed to a distributed pattern of activation rather than a single analog value. Then, we suggest that a Hebbian scheme may establish the appropriate correlations between head direction and perceptual/hippocampal inputs. This way, the module could also make use of compass points (landmarks at an infinite distance; thus their allocentric bearing never changes) when available.

Another natural extension to the model is to allow flexiblity in choice of landmarks and reference point for newly recruited units. The selection could be modulated by factors such as the landmark's perceptual salience, and its stability across trials. This way, more place units would be allocated to code for more informative landmarks. We believe this will allow us to provide a computational account of the "cue set" phenomenon.

Although not addressed in the present model, we believe that tactile and other sensory cues may take the place of visual input to place cells, allowing the place cells to check the path integrator's results and make corrections if needed. For example, a corner in a maze will have geometric qualities apparent to the animal via its whiskers. Upon recognizing this corner, the place system could adjust the path integrator output to more precisely match the learned coordinates of the corner in the active reference frame.

While corners and walls can be viewed as salient landmarks, they are not necessarily uniquely identifiable. The current model requires perceptual inputs to be distinct. Thus, it is unable to cope with any potential ambiguity. The hippocampus might be providing the contextual encoding that enables such configural discrimination [Sutherland & Rudy 1989]. Providing a computational account of this process remains an open problem.

Our model leads to the following prediction: place cells should briefly lose their direction sensitivity when an animal is first released at a random spot in a familiar environment. The reason is that the path integrator is not producing valid output, so place cells must be controlled by visual inputs alone. Only after the animal recognizes its location and resets its path integrator can place cells again become controlled by an active reference point set. While some preliminary observations are consonant with this conjecture (O'Keefe, see above), quantitative experimental data are needed to validate this prediction.

Conclusion

We have proposed a computational theory of rat navigation based on coupled mechanisms for path integration, place recognition, and maintenance of head direction. Our theory accounts for the following phenomena: (1) place cell activity reflects location in the environment; (2) place cell activity anticipates position during locomotion; (3) place cells continue their activity in the dark; (4) reset of head direction is dependent on visual cues; (5) place cells are robust against deletion of landmarks; (6) disruption of place cell response occurs after transposition of landmarks; (7) place cells can develop direction sensitivity in routine contexts; and (8) loss of direction sensitivity occurs as a response to novelty.

A variety of problems remain to be addressed. Although our theory makes frequent reference to place cells and the hippocampus, it is not yet a neural-level theory. We have not proposed a specific location for the Local View module, for example, nor speculated on why head direction sensitive cells are found in at least five separate locations in the rat brain (Taube, personal communication). Before tackling these questions, additional computational issues need to be settled. Chief among these are the role of geometric and tactile properties of the environment in determining place codes, the influence of a learned *cue set* on perception, and the mechanism by which cue sets are shaped by experience.

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