

opens⁹. What learning flight and sequence of recorded views underpin such precise targeting?

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Primer

Neuroethology of spatial cognition

Paul A. Dudchenko^{1,*} and Douglas Wallace²

A key challenge for animals is recognizing locations and navigating between them. These capacities are varied: we can remember where our car is parked at the mall, rats are able to remember where their nest location is while foraging for food morsels, and bats are able to fly directly to a favourite fruit tree 20 kilometers from their home cave. These spatial abilities, whether commonplace or remarkable, raise fundamental questions. First, how do animals find their way? Second, how does the brain represent the outside world?

In this Primer, we will address both questions from the perspective of rodent cognition and neuroscience.

Rodent behavior basics

Rodents, particularly rats and mice, are much studied as model organisms for understanding basic mammalian brain processes and, increasingly, disease states. At the beginning of the 20th century, rats were used to answer basic questions about learning and memory, often using mazes. Much is now known about their behavior and neural systems, but it is useful to consider their natural behaviour – or at least the unstructured behaviour of a laboratory rat foraging for food – on an open platform.

Exploration

Rats are cautiously curious. If you were to place a rat on a table, in the absence of strong light (which they

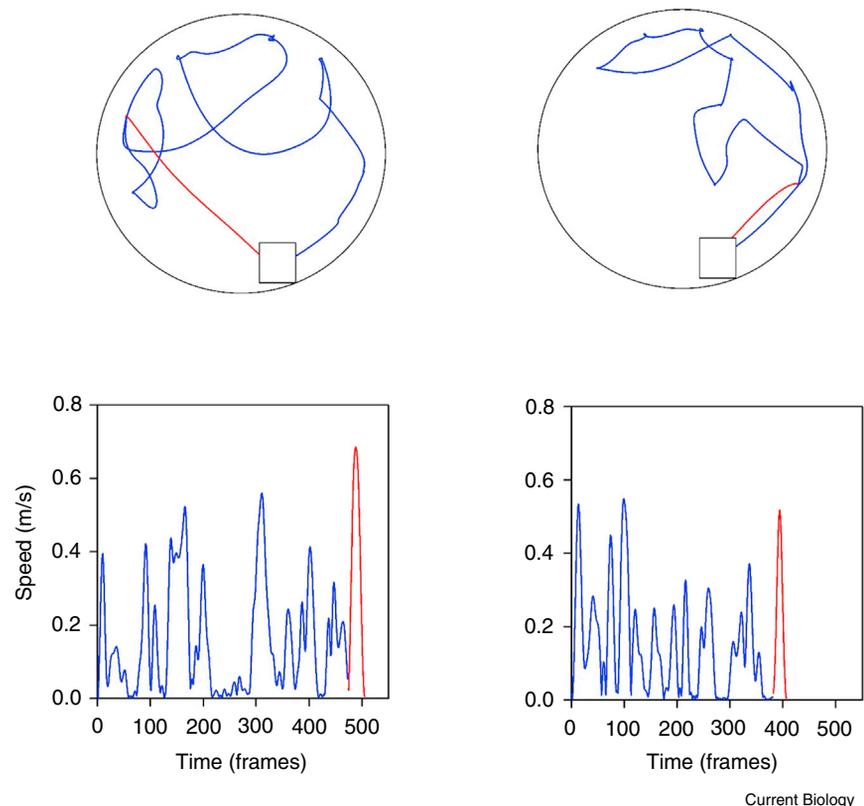


Figure 1. Topographic (top panels) and kinematic (bottom panels) characteristics plots for two representative exploratory trips by a rat.

The outward segments (blue lines) are a set of slow, relatively non-circuitous progressions punctuated by stops of varying duration. The homeward segment (red lines) is a single progression with peak speed at the midpoint of the journey and magnitude scaled to the Euclidean distance to the home base. Longer homeward segment Euclidean distances elicit faster peak speeds (left panels), whereas shorter homeward segment Euclidean distance elicit slower peak speeds (right panels).

find aversive), it would engage in bouts of movement that gradually cover more of the environment. Each bout would typically conclude with a return to the point where the rat was placed into the environment. Ian Whishaw and colleagues have shown that, if a feature of the environment affords protection, the rat adopts this as a home base; otherwise, it uses the introduction point as a home base. Mice are also inclined to establishing a home base in an open platform environment, with visual, tactile and olfactory cues influencing the position of the home base (Gorny *et al.*, 2002; Clark *et al.*, 2006). For rodents, the location of the home base is typically marked by grooming, rearing, and circling behaviors (Eilam and Golani, 1989). Once the home base is established, all subsequent behaviors are organized around this location.

Behaviors observed after home base establishment are kinematically and topographically organized. For example, movements away from the home base are slower and more circuitous relative to movements towards the home base (see Eilam, 2014, for review). This organization allows division of exploratory behavior into a sequence of trips focused on the home base (Whishaw *et al.*, 2001; Wallace *et al.*, 2006). The initial or outward segment of these trips involves relatively slow, non-circuitous progressions, punctuated by stops of varying duration and by changes in heading (Figure 1). The terminal or homeward segment follows the last stop and is a fast, non-circuitous path that ends at the home base. Although features of the environment can influence this behaviour, for example walls can elicit thigmotactic behavior, this organization is a ubiquitous characteristic of rodent open field behavior that may extend to humans (Blumenfeld-Lieberthal and Eilam, 2016).

Rats use path integration — an internal tracking of movements — to organize exploratory behavior. In path integration, self-movement cues generated as the rat moves away from the home base are used to update a representation of current position. Spontaneity in homeward segment initiation suggests that rats use this

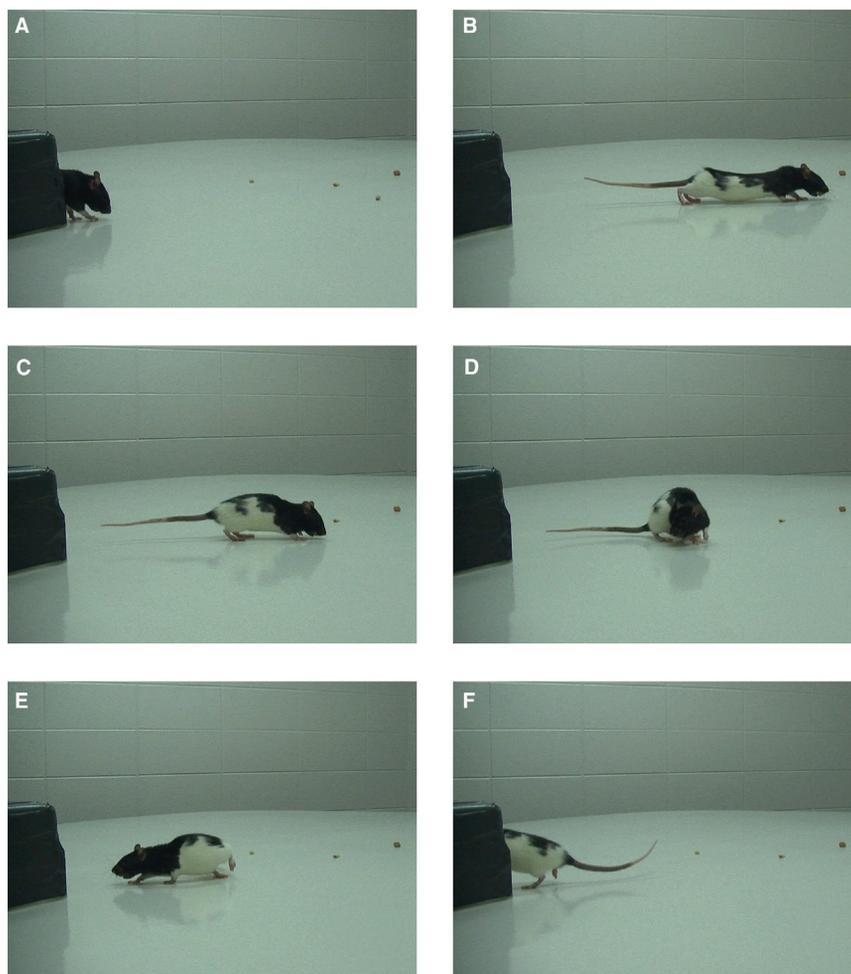


Figure 2. Food hoarding in the rat.

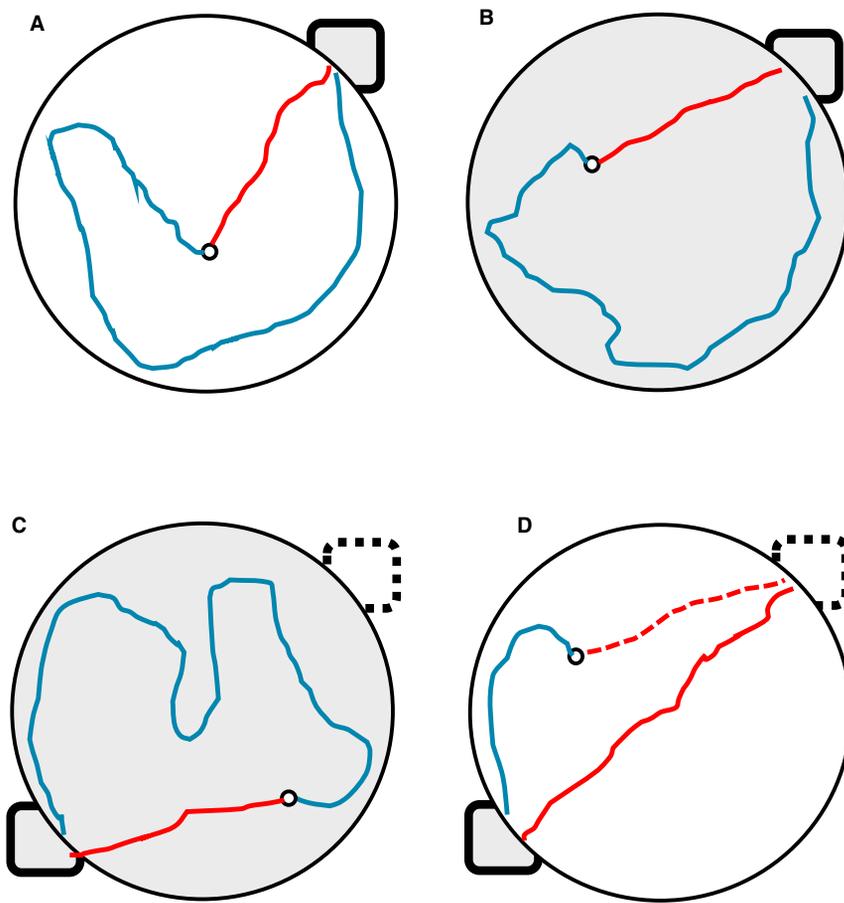
The rat exits the home base (A) to locate a food item (B). Upon locating the food item the rats will use a combination of environmental and self-movement cues to guide movement toward the refuge (C–E). The rat will enter the home base prior to consuming the food item (F).

online representation to estimate the direction to their home base rather than encoding a fixed sequence of progressions and turns, or a route engram. This representation may also be used to estimate distance. For the homeward journey, peak speeds cluster at the midpoint and scale to the Euclidean distance of the path, indicating that rats use distance estimates to guide return behavior. Neither direction nor distance estimates require environmental cues. Normal exploratory trip organization is independent of access to room- or home base-associated visual cues (Wallace *et al.*, 2006). Further, removing the physical home base during an exploratory trip (Whishaw *et al.*, 2001) or damaging olfactory bulbs prior to an exploration session

(Hines and Whishaw, 2005) does not impair exploration around the position of the home base. This indicates that potential home base odor cues are not necessary to guide exploratory behaviour, and suggests that path integration-based self-movement cue processing is sufficient for exploratory trip organization. As the novelty of the environment abates, the frequency of exploratory behavior declines, and the willingness to eat or to carry food to a home base increases.

Homing

Rats readily search familiar environments for randomly located food items. Upon finding a food item, rats will carry it directly to an established home base if the estimated consumption time exceeds



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Figure 3. Homing in the light and the dark.

Representative outward (blue lines) and homeward (red lines) paths are plotted for food hoarding behavior under various conditions. The hidden probe (A) involves testing under light conditions with the home base located below the surface of the table. The dark probe (B) involves testing under dark conditions with the home base located below the surface of the table. When the location of the home base is shifted to the opposite side of the table in the dark (C), rats are still able to make a direct return to it, indicating that they are able to track their movements in the dark. However, if the home base is moved in the light (D), rats return to the former location of the home base first, before then moving to the new location. This suggests that the rats use an association between the home base and visual landmarks beyond the table to guide their homeward journey initially, and then use path integration once they discover that the base has been shifted.

estimated carry time (Whishaw, 1990). Similar demonstrations of homing have been described in the female desert mouse (Mittelstaedt and Mittelstaedt, 1980) and the golden hamster (Etienne, 1980). In the field, deer mice have been reported to return to a home base even following displacements of 1.2 kilometers (Calisher *et al.*, 1999).

To identify the basis of homing, laboratory studies by Ian Whishaw and colleagues have used a table-top task where a submerged home base is placed on the periphery of

a large circular table. Under normal illumination, a rat will leave this home base, forage for a food reward that has been placed in a random location on the table, and then make a direct return to it to consume the reward (Figures 2 and 3A). As the homeward path does not retrace the outward path, the rat is unlikely to have followed an odor trail to the home base.

In the dark, rats also return directly to the home base once they've found the food reward (Figure 3B). This indicates that any visual cues

associated with the home base are not necessary for identifying its location (though they may be used in the light). Also, as described above, rats return to a home base following an exploratory journey even following the removal of their olfactory bulbs, which suggests that odor cues are not necessary to guide movement towards the home base. If the base is moved to a new location on the opposite side of the table, rats still make a direct return to it (Figure 3C). This capacity to return to the home base in the dark regardless of its location is consistent with the use of path integration for homing. A slight wrinkle occurs when the home base is shifted to a new location in the light (Figure 3D). In this instance, the rat first returns to the former location of the home base, before moving to its new location. As the animals were trained with the home base in the former location, their initial return to it suggests that associations with visual cues in the room guide homing in a familiar environment. The ensuing correction to the new home base location, moreover, indicates that putative self-motion information is still available to the animal, albeit as a secondary source of information.

Alternation and perseverative behavior

Rodent behavior also depends on the environment. On dry land, rats will alternate between visited locations, and this is the foundation for many spatial tasks used to investigate mnemonic processes. For example, different types of memory have been dissociated using the radial arm maze, an apparatus in which several maze arms radiate from a central platform. In one form of the maze, food reward is consistently located at the end of a subset of arms. Rats learn to visit only the baited arms, demonstrating reference memory, and do not return to a previously visited arm, which reflects the use of working memory. The rats adopt a win-stay strategy, returning to a rewarded location, if the reward encountered at the end of a maze arm is not exhausted in a given visit. In aversive, water-based tasks, such as the Morris water maze, perseverative responding facilitates learning the location of a hidden

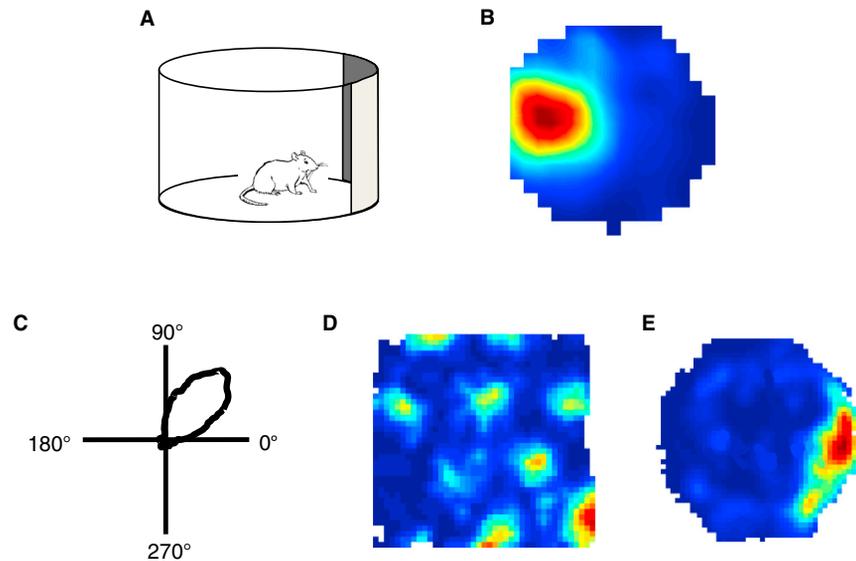
escape platform (Whishaw and Pasztor, 2000).

Landmarks, environmental shape and path integration

Rodents use multiple sources of information to navigate. For the most part, these have been identified in careful laboratory studies, where the number of cues available to the animal is limited, and manipulation of specific types of cues, such as visual landmarks, is possible. Broadly, rodents (and humans), preferentially use visual cues at the edge of the perceived environment for orientation. Under certain conditions, the shape of the environment can be sufficient for identifying locations (Cheng and Newcombe, 2005). Rat eyes, however, lack foveas, and the rat's visual acuity is much less than that of a human; furthermore, the rat's eyes are laterally placed, and not precisely coordinated with one another. Thus, rat vision consists of two overlapping monocular fields, and appears to be particularly tuned to detecting moving overhead stimuli (and, presumably, predators; Wallace *et al.*, 2013). As described in the discussion of behavioural studies above, in the dark or in the absence of a salient visual cue, rodents can use self-movement cues — vestibular, proprioception, optic flow — to keep track of their location as they move about. In addition to the use of vision, geometry, and self-motion, rats can follow odor trails left by other rats, or by the experimenter (Wallace *et al.*, 2002).

Place cells, head direction cells and grid cells

As is clear from the preceding discussion, rodent spatial behavior is structured, and rodents can use many cues to identify their location. But there is another reason why rodent spatial cognition is of interest: one of the success stories of contemporary systems neuroscience is the discovery of neural circuits in the rodent brain dedicated to the recognition of locations and headings (Moser *et al.*, 2017). In the early 1970s, John O'Keefe and Jonathan Dostrovsky described neurons in the hippocampus which fired when an animal occupied a specific location within its environment (Figure 4B).



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Figure 4. Spatially tuned neurons in the rodent brain.

(A) In the laboratory, recording of spatial neurons has often been conducted in a cylindrical environment with a cue card affixed to the wall to provide orientation. (B) Overhead view of a hippocampal place cell firing field in such an environment. Recordings are conducted over several minutes, and a color-code rate map show areas of the cylinder floor where there neuron fired at a high rate (warmer colors) and where no firing occurred (dark blue). (C) Polar plot of a head direction cell. This cell fired when the rat faced about 45°, and little firing was observed when the animal faced other directions. (D) Example of a grid cell. First described in the medial entorhinal cortex, these cells exhibit multiple, hexagonally arranged firing fields (example courtesy of James Ainge). (E) Example of a boundary-vector/border cell (example courtesy of Anna Smith).

These ‘place’ cells tiled the animal's environment: different cells have different place fields — locations in which they fired — and together they provide a representation of the entire environment. This phenomenon, together with evidence from studies of the effects of hippocampus damage, led O'Keefe and Lynn Nadel to argue that the hippocampus provided the neural substrate for a cognitive map.

In the late 1980s, James Ranck Jr described a second class of spatially-tuned neurons which fired when the rat faced a specific direction. These ‘head directions’ cells were shown in careful experiments by Ranck, Robert Muller, John Kubie, and Jeffrey Taube to be anchored to the animal's external environment, and fire over about a 90° range (Figure 4C). Subsequent work by a number of investigators showed that these cells were found in an interconnected set of brain structures, ranging from brainstem nuclei to regions of the cortex.

More recently, the lab of May-Britt and Edvard Moser described neurons

in the entorhinal cortex — an input structure to the hippocampus — which exhibited multiple, hexagonally arranged firing fields (Figure 4D). Strikingly, the size of these ‘grid’ cell fields and their spacing vary along the medial entorhinal cortex, in a manner that matches the change in size of place fields along the hippocampus dorsal-ventral axis, suggesting a close tie between the two.

Other spatially-tuned neurons include ‘boundary-vector’ or ‘border’ cells, described by Colin Lever and colleagues as well as the Mosers. These appear to fire at a specific distance and direction from a boundary, for example a maze wall (Figure 4E). The existence of such cells was predicted by Neil Burgess and colleagues, who argued that such representations could give rise to place cells. There are also cells in the medial entorhinal cortex that encode the speed of the rodent's locomotion (Kropff *et al.*, 2015). Such cells could contribute to the animal's ability to path integrate, by indicating the distance travelled in a given time.

Lastly, again within the medial entorhinal cortex, there are ‘object-vector’ cells, whose firing is tuned to a distance and direction from an object within an environment (Høydal *et al.*, 2017). Earlier work by Deshmukh and Knierim (2013) observed a potentially similar phenomenon: ‘landmark-vector’ (place) cells within the hippocampus. How object- and landmark-vector contribute to navigation is not fully understood, but it is not hard to imagine that they provide one means of identifying local locations.

Together, the representations described above appear to provide many of the essential elements for the recognition of locations, the tracking of movement, and potentially the linkage of environments beyond the animal’s immediate vista. The brain regions involved may well serve similar functions across species, as there is evidence that the hippocampus, for example, varies in size for food-caching birds, suggesting that this structure’s volume reflects spatial memory demands (Clayton, 1998).

The challenge of long-range navigation

As described above, a good deal is known about rodent exploration and spatial cognition in laboratory-scale environments. In parallel, the elements of a neural representation of space have also been identified, again almost exclusively from controlled laboratory environments. Correlations between the responses of neural representations and spatial behaviour have been observed (e.g., Butler *et al.*, 2017), though not in every instance (Weiss *et al.*, 2017). A challenge is to link these behavioural and neural observations with navigation over distances encountered in the wild (Poucet, 1993).

One answer may be that as the rodent moves from one location to another, it links the representations of each (for example, Taube and Burton, 1995; Dudchenko and Zinyuk, 2005; Carpenter *et al.*, 2015). In this way, local representations give rise to larger, global maps. With a stable direction frame provided by head direction cells, it’s possible that place

and grid representation come to represent the entirety of an animal’s locomotion.

As argued by Geva-Sagiv *et al.* (2015), however, the resolution of place cells in small environments is not suitable for long range navigation. Their proposal, based on elegant studies in the bat from Nachum Ulanovsky and colleagues, is that space is represented at different scales, and over longer distances, place cell fields are considerably larger.

Together, head direction, place and grid cells may link independently perceived environments with a consistent directional heading and represent locations at different scales, allowing efficient navigation over a range of distances and environments. Such a neural architecture may allow a representation of space (and of the locations of others; Omer *et al.*, 2018) that is anchored to the external world, updated by the animal’s motion, and fit for recognizing locations and navigating between them.

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