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Rodentia Navigation

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Synonyms

Acquisition of knowledge about spatial location;
Spatial learning

Definition

Rodentia navigation refers to how rodents find
their way about (i.e., to find food or water, or to
return home), to the many strategies and mecha-
nisms underlying spatially guided behavior.
Rodents have a varied range of strategies, some
innate and others learned, that help them to navi-
gate, and when faced with a specific spatial task,
the one they choose will depend both on their
sensorial capacities and on the nature of the stim-
uli that are available (for reviews see Rodrigo
2002; Tommasi et al. 2012).

Background

Rodents can use different navigational strategies
to locate a goal. Moreover, they can use a given
strategy in a specific situation and under different
conditions, use another one. The ability to find
their way round their world is seen as of critical
adaptive significance. Rodents can navigate using
information based on conspecifics (social influ-
ences), on their own movement (i.e., dead reck-
oning or path integration), on a single beacon or
landmark, on multiple landmarks (which includes
geometric encoding), or they can navigate using
information based on the relationship of multiple
landmarks (i.e., which is often called "a cognitive
map"). Rodents can also use a visual matching
strategy. In the last decades, there has been a great
interest in discovering the navigational strategies
they use, the conditions for using each strategy, as
well as understanding the neural mechanisms of
navigation. The most interesting results have been
obtained with gerbils and with rats. Rodents are
usually considered to be burrowing animals. They
use their burrows for different purposes (e.g., to
storage food and to escape from perceived
threats). A number of behavioral examples will
be reviewed below.

Social Influences on Navigation while Foraging. A Case of Episodic Memory?

Learning from other conspecifics is important for
many animals and the spatial domain is not an
exception. Rats begin their search for food from a

central point, their burrow. This characteristic makes the exchange of information with their conspecifics crucial in order to determine where food is located.

In social interaction, the information is transmitted through olfactory cues. Moreover, rats have the ability to detect if their conspecifics have eaten recently as well as what they have eaten, which can lead to a preference for a particular food in a specific spatial location. Therefore, social interaction can facilitate where food is located (Galef 1988).

Social influences while searching for hidden food has been much studied recently using different arenas as well as the radial maze, where choices are determined by spatial location (Brown 2011). For example, a recent study by Bisbing et al. (2015) examined the conditions under which the spatial choices of rats searching for food were influenced by the choices made by other model rats. The results showed that the social influence could be very strong under at least some conditions; they support the claim that the information that an animal acquires directly from its own experience with the environment (personal information) as well as the information provided by model rats (social information) are important. However, social information about the food location could influence spatial choices only when the social cues provided information that was not redundant with the information provided by other nonsocial cues. The clear implication is that the social cues and other kinds of stimuli seem to share the same or similar conditions, basic effects, and mechanisms. Both sources of information can be used in a flexible and adaptive way to guide choice decisions.

Are the previous examples a case of episodic memory, of memory based on conscious recollection? Could the rats remember the integrated "what," "where," and "when" information from specific past events? A very interesting approach to understand episodic memory in rats involves what is referred to as "source" memory (also called source monitoring). Source memory refers to memories about the conditions under which a memory was acquired (see Jonathon Crystal in the present issue).

Dead Reckoning or Path Integration

Dead reckoning or path integration refers to the process by which animals keep track of their current position in relation to a known position by using internal vestibular and kinaesthetic information, that is, information based on their own movement. To do so, they continuously process information about changes in distance and direction at the different points of their path. For example, Mittelstaedt and Mittelstaedt (1982) placed mother gerbils and their pups inside a nest that was at the edge of a large circular arena. The pups were then caught and displaced to a hole in another part of the arena. They observed that the mother soon began to search for the pups and that as soon as she found them, picked each one up in her mouth, and went straight back to the nest. The gerbils performed equally well in conditions of total darkness and when the outward path had zigzags and detours. The best demonstration accomplished by dead reckoning comes from experiments on displacements. Mittelstaedt and Mittelstaedt (1982) rotated the edge of the arena while the mother gerbil was in the hole, so that the nest was displaced. They observed that the mother gerbil returned to the place where the nest had been previously, demonstrating that the homing performance was not based on a cue present in the nest, but rather one based on path integration. They also observed that if the hole was rotated strongly while the mother and their pups were inside, the mother compensated for the rotation and headed straight back to the nest. However, if they rotated it or displaced it slowly sideways, the gerbil did not compensate and was disoriented. Similar results have also been obtained with golden hamsters. Although path integration can often be a very effective homing mechanism, it also has limitations. Both random and systematic errors often occur.

Navigation Using a Single Beacon or Landmark

Path integration tends to accumulate errors. Therefore, most rodents tend to use external landmarks to locate themselves or their goals. Preferably, they use proximal cues or beacons. Beacons are objects situated so near the goal that the animal

simply has to perceive them in order to locate the goal. For example, Morris (1981) trained rats in a circular pool full of opaque water. Some of the rats could escape from the water by climbing up onto a black platform which was a centimeter above the level of the water. Under these conditions, the platform functioned as a beacon. The rats, good swimmers but not very fond of water, quickly learned to escape from the water by climbing onto the platform from different points of the pool. In the presence of a beacon, all the animals have to do is orient themselves and approach. For this kind of navigation, rodents only need to associate the stimulus-goal (or a stimulus that is close to the goal) with the reinforcer.

But landmarks are normally far away. Distal landmarks are fixed singular objects situated further away from a goal than a beacon is, but which are still close enough to provide some information about the distance to the goal. If they are asymmetrical, they can also provide directional information. Finding a goal (i.e., determining both direction and distance) on the basis of landmarks is called "piloting" (Cheng and Spetch 1998). A very influential study was carried out by Collett et al. (1986), with female gerbils. The animals learned to dig for a sunflower seed buried in bedding, with a cylinder landmark placed at a fixed distance away. The gerbils learned to search in the correct location based on the landmark. To locate a goal based on a landmark, an animal has to perceive the distance and the direction of their position with respect to the landmark, to remember the distance between the landmark and the goal and its direction, and then to calculate the distance and direction from its position to the goal. The authors used a single symmetrical landmark in these experiments, which is not enough to pinpoint the location of a goal. Such a landmark only indicates the distance to the goal, but not the direction. Thus, the animals must have obtained directional information from another source. Given that the landmark was moved from trial to trial, but always at the same orientation with respect to the experimental enclosure, possibly the gerbils were able to obtain directional information from some other cues (like a door or a window). Moreover, Collett et al. (1986) carried out different tests in which they changed the size of a landmark and observed that these changes did not affect the place in which the gerbils searched for food. These results showed that gerbils do take into account the distance between the landmark and the goal, regardless of the landmark's size.

Navigation Using Information Based on Multiple Landmarks (Which Includes Geometric Encoding)

In another experiment by Collet et al. (1986), it was shown that gerbils can use information about the relative position of several landmarks that maintained a constant relationship to a goal. Gerbils were trained in an arena, a sort of open field, to find hidden food in a place that maintained a fixed relationship with the position of two distinct and equidistant from the food landmarks. Following training (i.e., once they had learned to locate the food), a series of test trials were conducted. When one of the landmarks was removed, the gerbils searched in two locations whose directions and distances corresponded to those between each of the landmarks and the goal during training. This suggests that the animals knew the direction and distance of the food from the landmarks, but that they did not know the identity of the landmarks. Each landmark was treated as if it could have been either of the two training landmarks. In another test, the distance between landmarks was doubled and the gerbils searched in two places defined by the direction and distance of the goal from each of the two training landmarks. These results show that the gerbils, at least the females, calculated the distance and direction of the food from each cue independently.

Cheng (1986) was the first author to present evidence that rats can use geometric information to locate a hidden goal. He trained male rats in a rectangular arena, where the two short walls of the box and one of the long walls were black, while the other long wall was white. In addition, distinctive visual patterns were placed in each of the box's corners, as well as other nongeometric cues, like different odors. Food was buried in one corner of the box, and the rats had to search for it. Although rats learned to search in the correct location for the food, they made frequent

rotational errors searching in the corner diagonally across from the one where the food was hidden. The only characteristic that the target corner and the corner diagonal from it shared in common was having one long wall to the left and one short wall to the right, which implies that the information provided by the nongeometric sources of information to find the food location did not seem to be important. Cheng (see also Gallistel 1990) concluded that the rats used the geometrical framework of the box itself. Thus, what the rats learned was to search for food in the corner that had the long arm to the left and the short arm to the right. This would explain why the animals made rotational errors, since the corner diagonally opposite had the same properties. This experiment clearly shows that rats are sensitive to the geometrical relationships of a test environment. According to Cheng (1986) and Gallistel (1990), learning about geometric information (i.e., like the metric relations of distances and angles between a target place and the shape of an apparatus) occurs in a specialized module, which is impenetrable to nongeometric information. However, Miller and Shettleworth (2007) have claimed that changes in the associative properties of the geometric cues are governed by the same principles that apply to more traditional stimuli. Following these authors, geometric and featural cues (or landmarks) are separate elements, so that, for example, each corner in a specific apparatus has its own combination of the two kinds of cues, which are learned simultaneously and can interact (i.e., therefore, blocking and overshadowing, cue competition designs, are expected to occur). Well-designed experiments and different authors have confirmed the two previous outcomes with male rats (for a review see Pearce 2009).

Interestingly, in a pioneering study by Williams et al. (1990) with geometric and nongeometric cues, in which males and females were employed, a surprising result was found. Williams et al. (1990) trained rats in a radial maze. After they had reached asymptotic performance, the rats were tested following various manipulations to the geometry of the room or to the landmarks. Provided the geometry of the room was unchanged, males' performance was

unaffected by any change to the landmarks, but alteration of the geometry of the testing room disrupted their performance, even when the landmarks were still available for navigation. In contrast, females' performance was disrupted by rearrangement of the landmarks whether the geometry of the room was changed or not, although they were unaffected by the removal of the landmarks provided the geometry of the room was unchanged. A more recent study by Rodríguez et al. (2010) employed a different procedure to demonstrate rather similar effects. These results imply that a geometrical cue is more salient for males, while a landmark cue is more salient for females. A subsequent study by Rodríguez et al. (2011), where cue competition designs were used, confirmed this claim by showing that overshadowing is asymmetrical, both in males and in females. In males, geometry learning tends to overshadow landmark learning, but not vice versa; while in females, landmark learning tends to overshadow geometry learning, but not vice versa. Moreover, these effects were not influenced by the females' estrus cycle.

Subsequent work with male rats suggests that the relative salience of both cues (geometry and landmark) seems to be able to completely reverse the previous results (Kosaki et al. 2013; Mesa et al. 2017). Taken together, the clear implication of the previous studies is that the rules that govern learning about the shape of the environment (Cheng 1986; Gallistel 1990), or its boundaries (Doeller and Burgess 2008), are not necessarily different to those that govern learning about landmarks. Moreover, the study by Williams et al. (1990) was the first to show that the failure to consider sex as a variable while studying spatial learning can undermine the reproducibility of research findings. Hopefully this should be corrected in the future.

The distribution of two or more landmarks in space also has geometrical properties. There is evidence that rats can learn both the geometrical properties defined by a configuration of landmarks as well as the landmarks' identity (Greene and Cook 1997). Greene and Cook (1997) trained male rats in a modified open field in which a fixed configuration formed by six different objects was

presented to the animals. The rats searched for food, which was hidden in the upper part of several poles. Following acquisition, several test trials were conducted: with the same objects but in different positions, with different objects although occupying the same positions of the training objects, and with the training objects in their normal position. The results revealed that the number as well as the identity and the geometrical configuration formed by the objects were important factors when searching for food. Greene and Cook (1997) claimed that the animals learned the geometry formed by the objects and such learning included the objects identity as well as their specific position within the configuration they formed.

Navigation Using Information Based on the Relationship of Multiple Landmarks. The Cognitive Map.

Tolman (1948) was the first author to propose that animals form sophisticated representations of their environment and called this a cognitive map. Tolman conducted many maze experiments. We know that rats typically solve maze problems by learning to approach the place where the goal is. But how is this place defined? For example, how does a rat solve a T-maze problem? (see Fig. 1). Usually, food is placed in one of the two goal-boxes (GB+) and not in the other one (GB–), and the subject has to choose between one arm and the other at the choice point. This is a spatial discrimination task, and traditionally it has had two alternative explanations (i.e., place vs. response learning — classical conditioning vs. instrumental or operant conditioning). According to Tolman (1948), the rat learns to associate the correct goal-box, GB+, with food and the incorrect one, GB–, with its absence, so that after a certain number of trials it chooses the correct goal-box and avoids the incorrect one. On the other hand, according to Hull (1943), what the rat learns is to execute a certain response instead of another at the choice point, because the first one is followed by food while the second one is not. In both cases, it can be said that the animal has been conditioned, although for Tolman it is a case of classical conditioning, "place" conditioning (the
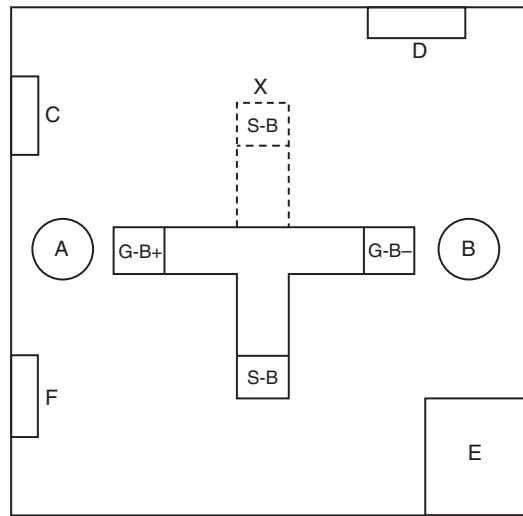
Rodentia Navigation, Fig. 1 A schematic diagram of a T-maze. S-B = start-box, G-B+ and G-B– the rewarded and unrewarded goal-boxes. *A*, *B*, represent distinctive objects immediately adjacent to the goal-boxes, and *C*, *D*, *E*, and *F* are various landmarks (doors, windows, tables) in the room. The dotted start-box and arm at X represent a new location for the start of a test trial. (After Mackintosh 1983 –with permission)

rats learn associations between places and rewards), and for Hull it is a case of instrumental or operant conditioning, "response" conditioning (one could say that the rats learn associations between responses and rewards).

The results have been generally in favor of place learning (classical conditioning), even when the maze is rotated 180^0. Tolman regarded conditioning as the acquisition of new knowledge about the world, instead of the acquisition of new responses or new reflexes. For him, the rats arrived at the correct goal-arm by using a cognitive map of the experimental room. But Tolman never explained the specific properties of the cognitive maps and gradually his theory lost credibility (O'Keefe and Nadel 1978).

In their very influential book, O'Keefe and Nadel (1978) claimed that rats can learn the correct trajectory to reach a goal in a maze in two ways. The main one, "true spatial learning," they label locale learning (or the "hypothesis of the cognitive map"). A rat solving a problem by locale learning would form a cognitive map of the environment where the maze is located, and

of the specific location of the rewarded goal-arm within that environment. A crucial feature of their account was that O'Keefe and Nadel (1978) consider that such learning is nonassociative, that it happens in an all-or-nothing way, and that it implies the formation and readjustment of a complete, global, representation of the environment in response to novelty. They also claimed that this kind of learning is highly flexible and that the hippocampus is the responsible cerebral structure. The second way to approach a goal they termed guidance learning. Learning by guidance implies approaching one specific cue or set of cues (a particular color, shape, odor or texture in the rewarded goal arm, for example, or a particular landmark or configuration of landmarks just behind the correct arm). Guidance learning was regarded as one form of taxon learning, the other being orientation learning, which is basically the same as Hull's response learning. Guidance learning is associative and can be regarded as a form of Pavlovian conditioning that does not depend on the hippocampus. It is also less flexible than true locale learning. These two strategies, locale and guidance, proposed by these authors to solve spatial tasks were traditionally understood as only one form of learning, place learning. However, O'Keefe and Nadel (1978) emphasized that locale and guidance strategies are two fundamentally different and independent forms of learning, each of them controlled by a different cerebral structure, and that only the taxon strategy, the guidance one, is controlled by associative laws. However, the following decades have demonstrated that their claims were not always correct. The two main ways of learning (locale and guidance strategies) are not independent, they interact. The clear implication is that knowledge about spatial location can be acquired in the same way as knowledge about other relations between events (for reviews see Chamizo 2003; Leising and Blaisdell 2009).

A critical test of a cognitive map (according to O'Keefe and Nadel's proposal) would imply that experience of the route A-B-C-D not only would give knowledge of the direction and distance between A and B, B and C, and C and D, but would also be sufficient to allow deduction of the distance and direction from A to D in the absence of any experience of the direct route from one to the other. Very few experiments have shown this with rodents, although one by Roberts et al. (2007) is worth mentioning. In the study by Roberts et al. (2007), male rats were allowed to travel selected routes along the internal alleys of a cross-maze that led from one distinctive end box to another. A critical feature of this set of experiments was that only the internal geometry of the maze could be learned and used to travel between one end box and another. After an initial exploration phase, rats were given novel routes and shortcut tests that involved unknown peripheral alleys, that the rats had not used before. The animals chose the correct novel path or shortcut significantly above chance. These findings suggest that rats were able to compute novel routes and shortcuts within the maze on the basis of limited experience with the internal geometry of the maze. This study further shows that rats could link a place with a number of other locations when allowed to travel a single linking pathway.

Navigation Using a Visual Matching Strategy. An alternative account to the cognitive map hypothesis has shown that geometry can be less important that initially thought in rats. It refers to a snapshot (mental image) account of rat navigation, which is most important when animals are at a goal or near it (Cheung et al. 2008). According to Cheung et al. (2008), search behavior can be explained by assuming that the animals take a snapshot at the goal or near the goal. Then, on subsequent journeys to the goal, they will move in a way to minimize the difference between the memorized image and its current view. Cheung et al. (2008) proposed that mental snapshots are global in nature and involve a panoramic view of the entire environment; they include information about the spatial relationships between the different elements (i.e., distant from the goal landmarks or other featural cues) they contain. All that is required for an animal to be able to find a goal is that it can see at least a portion of the elements contained within a specific snapshot. This procedure based on the coincidence of images does not require an explicit learning of the landmarks or of

the spatial geometry of the environment in which the goal is located. These cues are implicitly contained in the panoramic images taken by the animal and their relative salience will determine if the differences between the images perceived by an animal will be dominated by geometry or by features or landmarks. Subsequent research has revealed that mental snapshots can also refer to local cues (Gilroy and Pearce 2014).

The term "cognitive map" is nowadays used in many ways, so that depending on the author it can mean very different things. Following Mackintosh (2002) this term has lost explanatory value. What is needed instead is to ask what are the mechanisms underlying any particular example of spatially guided behavior. Many questions remain to be answered.

Cross-References

- ▶ Bennett G. Galef
- ▶ Blocking
- ▶ Classical Conditioning
- ▶ Cognitive Map
- ▶ Dead Reckoning
- ▶ Discrimination Learning
- ▶ Episodic Memory
- ▶ Foraging
- ▶ Geometric Encoding
- ▶ Hippocampus
- ▶ Jonathon Crystal
- ▶ Landmark
- ▶ Learning
- ▶ Local Versus Global Features
- ▶ Morris Water Maze
- ▶ Open Field Test
- ▶ Operant Conditioning
- ▶ Overshadowing
- ▶ Path Integration
- ▶ Place Versus Response Learning
- ▶ Spatial Relations

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