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Route and landmark learning by rats searching for food

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ABSTRACT

Many foraging animals rely on visual landmarks and/or habitual paths to locate important resources. We examined the degree to which rats rely on these cues when they predicted conflicting food locations. In this foraging task, rats were required to find food which could be located using either a fixed route or a nearby visual landmark. In tests, we found that their subsequent search-based estimates of the food location were the same when animals had acquired a long-term memory of the route, the landmark, or both. We show that the degree to which animals rely on the cues depends not only on the discrepancy between the two cues, but also on whether animals can match the testing "view" with a learned "view" that has been acquired during training.

1. Introduction

The influence of visual landmarks on rodents' spatial learning has been examined in experiments using a relatively small spatial scale (cf. Biegler and Morris, 1993, 1996; Alyan and Jander, 1994; Collett et al., 1986; Etienne et al., 1990; Mittelstaedt and Glasauer, 1991). In the typical experiment, animals are trained to locate a fixed goal, starting from different points in the environment, using visual landmarks outside the experimental enclosure (O'Keefe and Nadel, 1978; Olton et al., 1979; Suzuki et al., 1980), distant boundaries or the environmental geometry (Cheng, 1986, 2008; Doeller and Burgess, 2008).

An increasingly important issue is the extent to which spatial learning is based on redundant navigational systems. For example, when animals travel repeatedly over a familiar area, other systems besides navigation by landmarks, begin to play an important role. Experiments using both ants (Collett et al., 2003) and homing pigeons (cf. Meade et al., 2005) show that both species develop highly stereotyped routes when traversing repeatedly to the same location, aiming at landmarks to recall an habitual trajectory. For example, Biro et al. (2004) showed that homing pigeons released from novel locations within a familiar area rely on highly preferred, stereotyped routes (Biro et al., 2006; Meade et al., 2006). Similarly, ants tend to develop fixed routes from their nest to a feeding site. The routes are initially shaped by learning views of a series of landmarks, with ants orienting to them along segments of the trip (Graham et al., 2003), a strategy referred to as view-matching.

Although spatial research in ants and homing pigeons has focused on route development over relatively long distances, it is possible that other species exhibit similar spatial behavior when traveling shorter distances. For example, Tamara et al. (2010) showed that rats develop fixed routes to a goal even in the presence of visual landmarks. Similarly, Collett (1987) found that gerbils continue their traveling direction, after they have initiated their trajectory, to aim at a landmark that has disappeared from its usual position. Although learning of a trajectory plays an important role in navigation, little is known about the role of landmarks when animals travel repeatedly to the same location. For example, Tolman et al. (1946a), working with rats in a "T" maze, showed that animals trained to develop a fixed response (i.e. turn left) in the presence of constant landmarks, depended on knowledge of the relation of the food and the landmarks rather than on the specifics of their previous learned response to find the food (a phenomenon referred to as place learning). Additional evidence, however, shows several circumstances in which directional and response learning occur more rapidly and readily than place learning (i.e. Skinner et al., 2003; Blodgett et al., 1949).

In a related line of research, path integration studies in small arenas have revealed that animals rely on visual landmarks when tested under light conditions, and on self-motion orientation cues when tested in complete darkness. More importantly, the reliance on each of these cues, visual and self-motion cues, depends on the degree of conflict between the two (Etienne et al., 1985). For example, hamsters trained to hoard food in an arena rely on a visual cue when there is a 90° conflict, but switch to route information when there is a discrepancy of 180° (Etienne et al., 1990). Importantly, experiments on path integration typically examine the use of a short-term memory of a route on spatial navigation. That is, animals must reset their path integrator after each excursion (Etienne et al., 1996).

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In the present set of experiments, we examined the influence of a long-term route memory on animal's use of a visual landmark. We hypothesize that repeated experience of a fixed route should allow rats a more precise localization of the goal and a decrease in cumulative errors induced by self-motion cues. Thus, animals' estimates of the goal location should be similar when self-motion cues, a visual landmark, or both types of cues, are available.

It is well established that rats show a strong tendency to form and follow trails (Calhoun, 1963; Tchernichovski et al., 1998), and to orient to large visual cues (Timberlake, 2002). We also know that rats follow fixed routes in a water maze when started from the same location over multiple trials (Tamara et al., 2010). Our interest in the present experiments was to determine whether rats' estimation of a goal location improves when both a route and landmarks are available, as compared to when only route or landmark cues are available. We also examined whether animals showed a preference for a visual cue versus a fixed route when there is a conflict between the two. We did this by repeatedly training animals to find a goal in the same location relative to the starting point and a visual landmark, and then testing whether they could find the goal without the landmark, or with the landmark displaced from its original location relative to the start position.

2. Experiment 1

2.1. Methods

2.1.1. Subjects

Experiment 1 was performed on 8 experimentally naïve female Sprague–Dawley rats, approximately 4 months old at the start of the experiment and housed individually in a colony room. The colony room was on a 12 h:12 h light:dark cycle. Before the start of the experiment, animals were food deprived to 85% of their weight. They were allowed constant access to water.

2.1.2. Apparatus

This experiment and all subsequent experiments were performed in a black, circular wooden arena measuring 1.67 m in diameter, and mounted on a wooden platform 1.14 m above the floor. All the experiments were conducted in the dark. Any cues outside the arena were reduced by a blue curtain surrounding the arena, hung from a circle of aluminum piping suspended from the ceiling. A heavy black vinyl curtain about 1 m from the circular blue curtain covered the walls of the room and masked any potential unintended cues. A 1 Hz LED light was placed on the opposite side of the arena from the starting point, and provided a visual landmark to the food's location. This visual cue provided both direction and distance information about the location of the food. A small number of food pellets (~6 pellets) were placed approximately 114.3 cm from the starting point (Fig. 1). Although the experiments were conducted in a dark room, we placed white confetti (~0.6 cm in diameter) on the floor over the arena, leaving uncovering only small sections of the floor, to prevent the rats from detecting the location of the food by sight. Rats were started from 3 (North, South, East) pseudo-randomly assigned locations. For each rat, the light and the food pellets were placed at a fixed position relative to its start location. To avoid any contribution of odor, we cleaned thoroughly the arena after every trial, and changed the start location.

2.1.3. Experimental protocol

The experimental procedure occurred as follows. At the beginning of each trial, animals were placed at the edge of the arena facing away from the center. In each trial we released the rat from the same starting point in the arena relative to the location of the food. Once the rat had found the food pellets, it was given time to eat them, and then removed from the arena and placed in a holding cage outside the experimental room. During training, three trials were conducted daily with an inter-trial interval of approximately 1 min. Between each trial, the arena surface was wiped down with an organic detergent solution to remove odor or food-related cues, and the starting point and the predictive light were rotated together to predict a new food location.

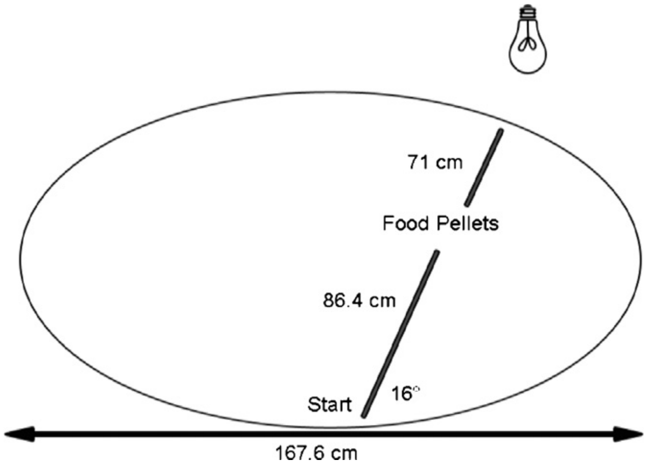

Fig. 1. Experimental set-up showing the location of the food and the light in Experiment 2. In Experiment 1 the food was located at 114.3 cm from the start.

After the first 11 days of training, the test phase was introduced. For all rats, on each of four days, two training trials were conducted followed by a non-rewarded 1-min test. In the first test, the light (landmark) was removed from the arena, and animals could only use the egocentric route to locate the goal (ER test). In the second test, animals were disoriented before the test (eliminating the use of egocentric cues) and the light was located inside the area (LDMK test). To disorient the animals, each subject was placed in a stand that could swivel either to the left or to the right with an opaque bowl confining the subject to the stand. Animals were rotated in the stand for 30 s followed by 30 s with the stand still. A complete rotation in the stand was completed every 5–6 s. In the third test, both the light and an egocentric route were available to the animals for locating the food (ER + LDMK test). In the last test, we examined the extent to which rats relied on the landmark versus the egocentric route by releasing the animals from a *new location* (West) thus creating a 90° conflict between the two types of cue (90° conflict test).

2.1.4. Tracking

A bank of red-LEDs and an infrared sensitive camera (connected to Noldus's Ethovision tracking software) were suspended from the ceiling to record the movement of each rat from the location it was released to the end of the trial. To facilitate inspection of the figures, the movement plots are presented as though the animals were always released from the South. All analyses were conducted in Matlab (Mathworks, Natick, MA).

2.1.5. Analysis

2.1.5.1. Training. During training we calculated the time it took animals to find the food location. We also calculated the efficiency of each path to the food as (a) the ratio of the bee-line distance to the actual distance moved by the animal, and (b) the straightness of each trajectory from Day 2 on (calculated by segmenting each path into 1 sec sections and calculating the straightness—see Batschelet, 1981). The mean vector length, r, provides a measure of how straight the path is. The closer r is to 1, the larger the degree of straightness. Day 1 was excluded from this analysis