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Research report

Traveling in the dark: The legibility of a regular and predictable structure of the environment extends beyond its borders

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ABSTRACT

The physical structure of the surrounding environment shapes the paths of progression, which in turn reflect the structure of the environment and the way that it shapes behavior. A regular and coherent physical structure results in paths that extend over the entire environment. In contrast, irregular structure results in traveling over a confined sector of the area. In this study, rats were tested in a dark arena in which half the area contained eight objects in a regular grid layout, and the other half contained eight objects in an irregular layout. In subsequent trials, a salient landmark was placed first within the irregular half, and then within the grid. We hypothesized that rats would favor travel in the area with regular order, but found that activity in the area with irregular object layout did not differ from activity in the area with grid layout, even when the irregular half included a salient landmark. Thus, the grid impact in one arena half extended to the other half and overshadowed the presumed impact of the salient landmark. This could be explained by mechanisms that control spatial behavior, such as grid cells and odometry. However, when objects were spaced irregularly over the entire arena, the salient landmark became dominant and the paths converged upon it, especially from objects with direct access to the salient landmark. Altogether, three environmental properties: (i) regular and predictable structure; (ii) salience of landmarks; and (iii) accessibility, hierarchically shape the paths of progression in a dark environment.

1. Introduction

The physical structure of the environment affects spatial behavior in animals [1–5] as well as in humans [6–8]. Accordingly, when studying how an internal (mental) image or map of the environment is constructed, it is necessary to also consider the physical structure of the environment as an independent variable. In humans, there are inherent difficulties in empirically studying complex and large-scale urban environments. These difficulties include the need to isolate the impact of specific urban features and to acquire data on the physical activity of individuals. Relying on the similarities between space perception in humans and animals [9], it was suggested to examine the relation between urban environments and spatial cognition by studying spatial behavior of rats in apparatuses that simulate urban structures [10]. The notion of comparing exploration and navigation in humans and rats is not novel. It originated in the studies by Tolman [11] and was further reconfirmed by the resemblance in the operative brain functions and in the mechanisms and strategies employed by humans and other animals when acquiring spatial information and establishing an internal representation, as revealed in past studies [9,12–15]. This notion was exemplified by testing rats in arenas that simulate a grid urban layout (e.g. Manhattan streets) and an irregular urban layout (e.g. Jerusalem streets), revealing that in the grid layout, rat movement was more structured and extended over a greater area compared with the restricted movement in the irregular layout. These movement patterns recall those of humans in respective urban environments, illustrating that the structure and shape of the environment affect spatial behavior similarly in humans and rats [10]. Spatial grid shape of the environment is in a sense reminiscent of grid cell activity in the context of spatial information processing. A specific grid cell fires whenever the animal's position coincides with any vertex of a regular grid, whereas a specific place cell fires when the rat is in a specific place [16]. Together with other neurons, the representation of place, distance and direction is acquired, permitting a continuous updating of metric representation of the animal's location [16,17]. The present study sought

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to hypothetically correlate the physical and neural grids by testing the rats' spatial behavior under a mixed grid and irregular physical environment structure.

Another physical property that shapes spatial behavior is that of the salience of landmarks. When available, the animals took longer paths that converged at the salient landmark, gaining accuracy at the cost of the increased path length [18–20]. The convergence of paths attested that the salient landmark became a target for traveling (beacon). Indeed, when a beacon was accessible, the animals diverted from the shortest path to their goal, instead passing by the beacon, which thereby shaped their paths. However, in order to exert the impact of a beacon, the landmark must stand out against the background of landscape [21]. In other words, it is not the physical structure of the landmark in itself that accounts for route convergence, but the contextual features, such as landmark spacing and density, that may turn a landmark into a beacon [21,22]. Considering that grid layout is ideal for ease of travel over an entire environment [10,23], the question arises as to whether a grid will mask the possible impact of a salient landmark. If so, it would imply that a regular and predictable structure of the environment holds greater advantage than the salience of a landmark.

Another principal physical property of locations in the environment is that of accessibility: higher accessibility to a landmark or location enables its approach from various locations and/or using a greater variety of paths. Poucet and Herrmann [24] suggested that in accordance with the 'topological encoding hypothesis', the accessibility (connectedness) of a specific location dictates the rate of exploration in that location. While this conclusion regarding 'connectedness' was derived from a study in a complex maze, in which each location had 1–4 specific connections, the manifestation of this property in a free-traveling agent has not yet been assessed.

The working hypothesis of the present study was based on a seminal study that analyzed the properties of urban grid road layout, in which it was claimed that "*the longitudinal streets all have individual character . . .each one is different – while the cross streets act as measuring devices . . .the sudden and particularly the rather indiscernible, shift to another grid system, or to non-grid, was very confusing.*" [8]. Specifically, here we tested rats in arena with half grid and half irregular object layouts. We hypothesized that in the arena with mixed grid and irregular object-layout, rats would travel more in the grid area. We also assumed that providing the rats with a salient landmark in the arena half featuring an irregular object layout would enhance travel in that sector, especially among the more accessible objects.

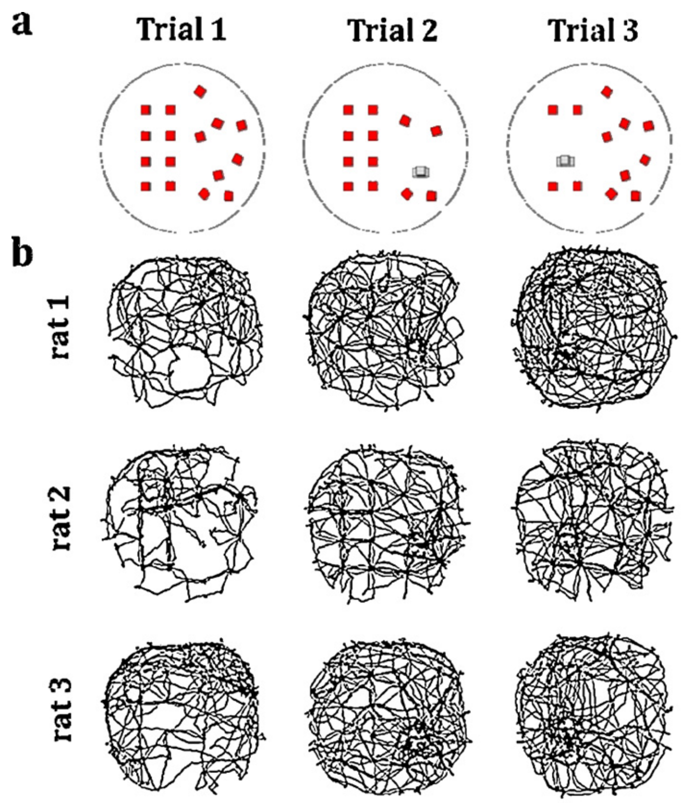

Fig. 1. The three trials that all the eight rats underwent (a) and the paths of progression in three exemplary rats (b). As shown, in trial 1 the left half of the circular arena included eight equispaced objects in a grid layout, while the right arena half comprised eight objects in irregular order. In trial 2, a salient landmark was placed in the right area, and in trial 3 the salient landmark was placed in the left area. As shown, the grid layout shaped the path of progression in trials 1 and 2 (left and central columns), whereas the impact of the salient object became apparent in trial 3.

2. Material and methods

2.1. Animals

Male Wistar rats ($n = 8$; age 3 months; weight 250–300 g) were housed in a temperature-controlled (24 °C) room with 12/12 h light/dark cycle (dark phase 8:00–20:00). Each two rats were held in standard rodent cages (40 cm × 25 cm × 20 cm) with sawdust bedding. They were provided with free access to water and standard rodent chow. Each rat was marked with a waterproof marker on its tail, and acclimated to 10-min handling each day for one week before testing. Rats were maintained and treated according to the institutional guidelines for animal care and use in research (permit L-10-013).

2.2. Apparatus

Rats were tested in a round arena, 200 cm in diameter, surrounded by a 50 cm high tin wall. The arena was placed in a temperature controlled (21 ± 1 °C), light-proofed room. Arena floor was covered in a navy-blue colored PVC layer. During testing the room was dark, with footage enabled by infrared light (Tracksys, IR LED Illuminator; UK) with an 830 nm wavelength filter, invisible to rats. Top-view of the entire arena was obtained via a video camera (Ikegami B/W ICD-47E, Japan) placed 2.5 m above the center of the arena and recorded on DVD device (Sony RDR-HXD 870, Japan). Sixteen identical objects (12 cm × 12 cm × 6 cm black-painted cement bricks) were placed in the arena in one of the following three layouts (Fig. 1a): (1) half arena with eight objects arranged in a grid layout with 25 cm between them, and half arena with eight objects arranged in an irregular layout with at least 25 cm between them; (2) half arena with a grid layout of eight objects (as in the previous layout) and half arena with an irregular layout of four objects and another 4 objects stacked to form a large salient object, 3-fold higher than the other objects; and (3) half arena with eight objects arranged irregularly (as in the first layout) and half arena with a layout of four orthogonal objects and another four objects forming a salient object as in the previous layout.

2.3. Procedure

In each trial, rats were individually released into the arena during their dark phase, when they are most active. A single rat was gently placed at a fixed start location next to the arena wall (topmost point of the arenas in Fig. 1a), and its behavior was then recorded for 20 min. All rats underwent testing in the three layouts over three consecutive days (one layout per day). All were first tested in the arena with mixed grid and irregular object layout; then in the arena with half grid/half irregular with a salient landmark, and ultimately in arena with half that included salient landmark and another half with irregular object layout (Fig. 1a). We did not include a control for repetitions since in a previous study in the same dark arena we found that rats did not change their spatial behavior over five repetitive exposures, even when repetitions involved local changes that did not distort the global geometry of the arena [25]. Upon completion of each trial, rats were returned to their home cage and the arena was wiped with detergent prior to the next trial.

2.4. Data acquisition and statistics

Video files were analyzed using 'Ethovision XT 7' (Noldus Information Technologies, NL) for tracking the movement of the rat in the arena, recording coordinates of the center of mass of the rat five times per second. For analysis, the arena was divided into the following areas: (i) *perimeter* – a 15 cm strip along the arena wall; (ii) *object* – a 25 cm × 25 cm square, centered on each object in the arena; (iii) *between objects* – the remaining central area of the arena not covered by the perimeter and objects; and (iv) *arena halves* – half of the arena area which includes the perimeter and eight objects in a layout. The following parameters were exported for further analysis using 'Microsoft Excel 2007': (1) *distance traveled* – the accumulative metric distance (m) traveled over a time of 20 min; (2) *duration at area* – the time spent at each of