

City rats: From rat behaviour to human spatial cognition in urban environments

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The structure and shape of an urban environment influence our ability to find our way about in the city¹⁻². Indeed, urban designers who face the challenge of planning environments that facilitate wayfinding³, have a consequent need to understand the relations between the urban environment and spatial cognition⁴. Previous studies have suggested that certain qualities of city elements, such as a distinct contrast with the background (e.g. The Eiffel Tower in Paris), or a clear morphology (e.g. the grid layout of Manhattan's streets) affect spatial behaviour and cognition^{1,5-7}. However, only a few empirical studies have examined the relations between the urban environment and spatial cognition. Here we suggest that testing rats in experimental environments that simulate certain facets of urban environment can provide an insight into human spatial behaviour in urban environments with a similar layout. Specifically, we simulated two city layouts: (1) a grid street layout such as that of Manhattan; and (2) an irregular street layout such as that of Jerusalem. We found that the rats that were tested in the grid layout covered more ground and visited more locations, compared with the restricted movement demonstrated by the rats tested in the irregular layout. This finding in rats is in accordance with previous findings that urban grids conduce to high movement flow throughout the city, compared to low movement flow in irregular urban layouts⁸⁻⁹. Previous studies revealed that the spatial

behaviour of rats and humans is controlled by the same underlying mechanisms¹⁰⁻¹¹. In the same vein, we show that rats demonstrate spatial movement patterns that recall those of humans in similar urban environments. Rat behaviour may thus offer an *in-vivo* means for testing and analyzing the spatial cognitive principles of specific urban designs and for inferring how humans may perceive a particular urban environment and orient in it.

In a seminal work¹, "The Image of the City", urban designer Kevin Lynch suggested that the legibility of the urban environment, which reflects the ease with which people understand and move about in a city, rests on the distinctiveness and coherence of five urban elements: landmarks, paths, nodes, districts and edges. Legible environments enable one to construct a mental image of the physical environment and thereby facilitate orientation and wayfinding¹. Lynch's seminal study provided an initial theory and method for unravelling the relations between spatial cognition and the physical environment, helping designers to plan urban environments while bearing in mind their usability and the need for a design conducive to easy orientation. Lynch's study was based on the intuition that the structure and shape of an urban environment greatly impact the way that people perceive it and find their way around. Despite the importance of understanding the relations between the urban environment and spatial cognition, there have been few other studies in this line^{7,12}. One is Hillier's "space syntax"¹³⁻¹⁴, which investigates the role of urban road systems in shaping human behaviour. Space syntax offers an analytical tool that represents space morphology as a network, providing quantitative measurements of parameters such as access or visibility. However, space syntax focuses on the centrality of segments (roads) in the urban road networks and its impact on collective human movement – leaving other morphological properties (e.g. Lynch's elements or grid pattern vs. winding streets) unexplained. Furthermore, it has been criticized for providing an explanation for

'how' people as a collective move, without answering the question of 'why' individuals move in space¹⁵. To answer the latter question it is necessary to take into account human spatial cognition, incorporating empirical research on the impact of the structure on movement.

Lynch's notion of the mental image of the city is reminiscent of the notion of a cognitive map introduced in the 1940s by the behavioural psychologist Edward Tolman¹⁶ in his seminal paper "Cognitive Maps in Rats and Men". Based on a set of experiments with rats in mazes, Tolman suggested that both humans and rats construct in their mind/brain a cognitive map that they use for orientation and wayfinding. Subsequent studies have further shown that both humans and other animals possess some form of internal representation of the external environment, and both seem to utilize similar mechanisms and strategies for finding their way¹¹. For example, path-integration is a navigational mechanism that, in the absence of visual information, enables the traveller (human or non-human, even a creature as 'simple' as an ant) to continuously track its current position in reference to a key point such as home or nest¹⁷. Similarly, both humans and animals utilize geometric properties of the environment for orientation¹⁸. Despite the above commonalities and the fact that Tolman's theory preceded Lynch's by two decades, Lynch never made the connection to Tolman's work and their theories and domains of study have never been integrated¹⁹. This led us to the idea that testing rats in settings that simulate urban landmarks, paths and other 'Lynchian elements', could provide new insights into human spatial performance in similar urban environments. Specifically, we sought to examine the potential of rat behaviour to serve as an *in-vivo* tool for assessing the legibility of specific aspects of urban forms.

In this study, we tested rats in a grid layout that resembled an urban grid layout (e.g. the Manhattan grid; Figure 1a, left), and in an irregular layout that resembled an irregular urban layout (e.g. the streets of Jerusalem or Boston's streets that parallel the banks of the River

Charles; Figure 1a, right). These test layouts represented two extremes with regard to their geometrical and topological properties, based on the convention that an urban grid layout makes wayfinding easy, whereas a complex irregular urban layout makes it more difficult^{1,8-9}. The simulated layouts were composed of 16 identical objects that were placed in a circular walled arena. The objects were either equally spaced in an orthogonal grid to simulate grid city layout, or irregularly spaced in order to simulate an irregular city layout (Fig. 1a). Two groups of naïve rats were each tested once ($n = 9$ each). At the beginning of testing, a single rat was placed in a specific location in the arena ('start point') and its behaviour was video-tracked for 20 minutes. The impact of these experimental layouts on the rats' movement is illustrated in Fig. 1b. As shown, 'grid rats' covered a greater area ($t_{16} = 2.90$; $P = 0.01$) and explored more objects ($t_{16} = 2.94$; $P = 0.01$) compared with the rats tested in the irregular layout. The travel paths of the 'grid rats' followed the array of objects, whereas the 'irregular rats' moved only in relation to the start point and its vicinity (Fig. 1b). Indeed, rats in the grid layout performed more trips between objects, while rats in the irregular layout performed more trips between the arena wall and nearby objects ($t_{16} = 9.80$; $P < 0.001$, $t_{16} = -8.67$; $P < 0.001$; respectively). Clearly, the above differences were not the result of differential activity, since rats in both layouts did not differ in their overall travelled distance ($t_{16} = 1.36$; $P = 0.19$). Altogether, our results show that while in both layouts the rats displayed the same level of activity, in the grid layout this activity was more structured in relation to object layout and extended over a larger area compared with the limited span and less structured activity of the rats in the irregular layout.

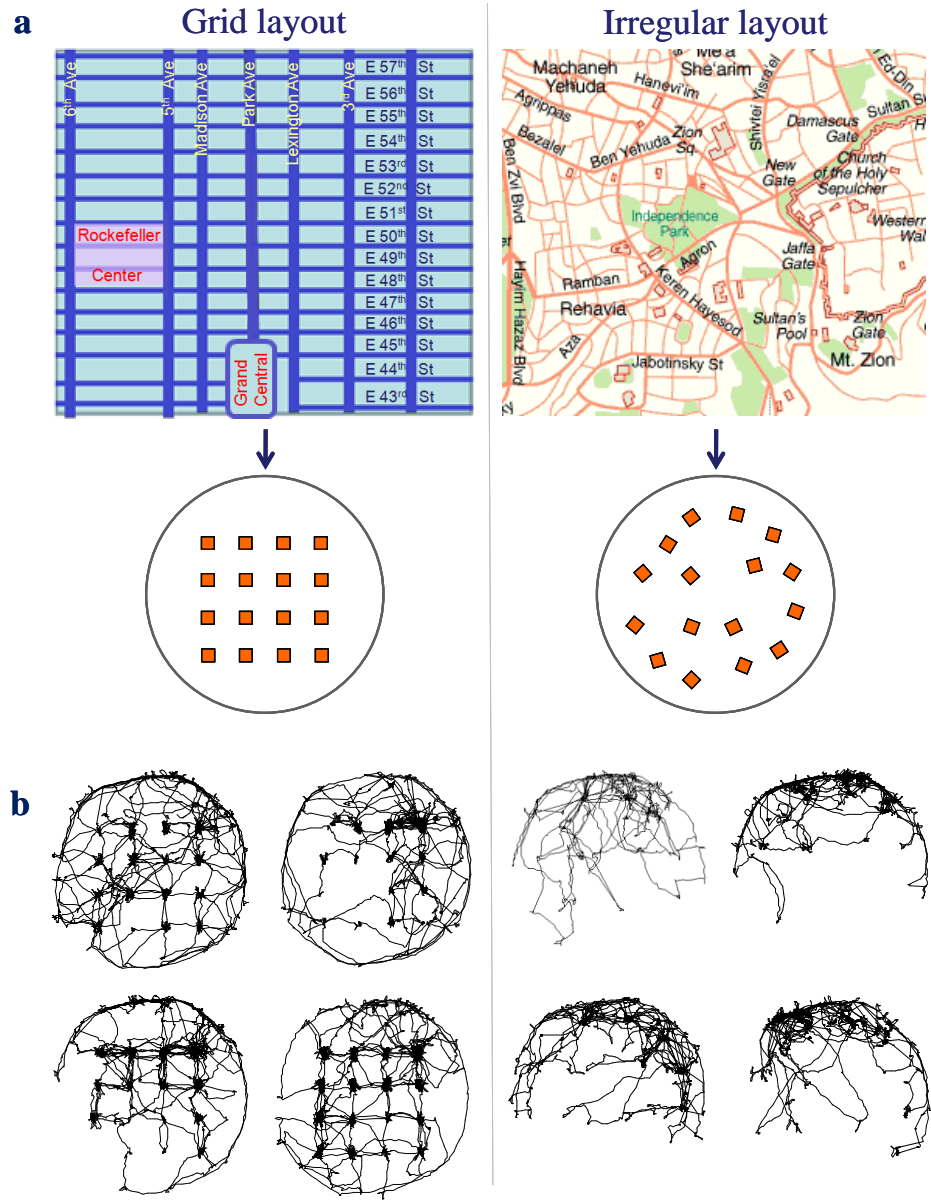


Figure 1: Grid and irregular city layouts, the respective test environments and the rats' paths of movement

a, The two simulated urban layouts and their respective test models: Manhattan (left), as an example of a grid layout; and Jerusalem (right), as an irregular layout. The arrow represents the start location at which rats were placed. **b**, Paths of progression of representative rats in each of the test environments, during the 20 minutes of testing. In the grid layout rat movement was dispersed throughout the arena, spanning the objects and the perimeter. In the irregular layout, rat movement was in relation to the start point and the nearby arena wall, covering only a portion of the arena area.

Humans, like other animals, explore, learn and find their way around by gathering information from the surrounding environment. Unlike animals, however, humans are distinguished by utilizing maps, signs and verbal directions. Nevertheless, they share with animals some similar mechanisms and strategies for spatial orientation^{10-11,17,20-21}. These mechanisms are revealed by the patterns of movement through the environment, since organization in time and space is the most reliable index of animal cognition²². The present findings demonstrate that the movement pattern of rats in an urban-like grid layout is more structured and extends over a greater area than the restricted movement of rats in an irregular urban-like layout (Fig. 1), resembling human movement in urban environments with similar, respective properties. Indeed, in humans, urban grids conduce to high movement flow throughout the city⁸⁻⁹. The ordered structure of the grid, with its coherent geometry, simplifies its perceived representation, and thereby supports orientation and wayfinding^{8,10,18,23}. In contrast, complex urban environments with many curves hinder access to local areas, and thereby restricts movement⁸⁻⁹. As in the aforementioned similarities between animal and human spatial cognition, it seems that here too the structure of the environment affects movement patterns similarly in humans and rats^{10,18}. Accordingly, we suggest that spatial behaviour of rats may be used as a tool to unravel aspects of urban design that affect spatial cognition in humans.

METHODS SUMMARY

Male Wistar rats (n = 18; age 3 months; weight 250-300 g) were tested in a round arena (200 cm diameter) enclosed with a 50 cm high tin wall. The arena was located in a dark, light-proofed room, and was illuminated with an infra-red light source, with an 830 nm filter that emits light

not visible to the rats. A video camera placed above the arena center provided a top view of the entire arena. Sixteen identical objects (12 cm x 12 cm x 6 cm) were placed in the arena. In the grid layout (Fig. 1a, left), the objects were placed in an equally spaced grid array (20 cm space between objects). In the irregular layout (Fig. 1a, right), the objects were spaced irregularly in the arena with at least 20 cm space between them and between them and arena wall. Rats were randomly assigned to one of the two test groups (n = 9 each), each tested in only one of the arenas. Testing was conducted during the night activity phase of the rats. The test began when a rat was placed at a fixed start point (Fig. 1a) near the arena wall, facing the centre of the arena. Its behaviour was then video-tracked for 20 minutes (Ethovision by Noldus, NL). After each test, the arena was paper-wiped with detergent. For analysis, the arena was divided into a perimeter area (a strip section 15 cm along the arena wall) and object areas (a circle 25 cm diameter around each object). Data of the two groups were compared by means of Student's *t*-test for independent samples.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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