Brief Communication

Generalization in Place Learning and Geometry Knowledge in Rats

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Rats were trained to search for a food reward hidden under sawdust in the center of a square-shaped enclosure designed to force orientation on the basis of the overall geometry of the environment. They were then tested in a number of enclosures differing in shape and in size (rectangular-, double-side square-, and equilateral triangle-shaped enclosures). Results showed that rats transferred their place-finding ability to the novel enclosures. Our results add evidence to the hypothesis that the evolutionary roots of spatial cognition entail a primitive encoding of geometric relationships, as already shown using other tasks in rats.

The concept of 'center' is straightforward in human communication, as it is one of those linguistic labels used to describe unambiguously the spatial structure of our environment. Moreover, the center has a special status in our perceptual world, and much has been written about its uniqueness in human visual perception (Arnheim 1988). Here, we show that 'the center' is recognized by rats searching for a hidden goal across a number of enclosed environments differing both in geometric shape and in size.

In many instances of spatial orientation, animals must make use of the spatial relationships (distances and directions) between landmarks or selected features of a given environment to determine the position of a hidden goal (Gallistel 1990; Thinus-Blanc 1996). The experimental situation described here consists of a case of piloting in an enclosed environment, where the geometry of the search space contains all of the sufficient information for animals to localize the goal. The central position was chosen ad hoc as the goal during training, starting from the assumption that the center can be unequivocally determined despite the size and shape of a regular enclosed space, thus providing a common locus of comparison for subsequent transfer tests in differently shaped enclosures.

To carry out these tests, it first had to be established that rats are capable of localizing the central position of an enclosure relying only on the spatial information provided by the geometry of the environment. Previous experiments showed that domestic chicks are capable of learning such a task (Tommasi et al. 1997; Tommasi and Vallortigara 2000). Moreover, experiments carried out using a triangular-shaped watermaze clearly indicated that rats can be trained to localize a submerged platform on the sole basis of environmental shape and also when the platform is located in the center (Pearce et al. 2001).

The subsequent step, and the main objective of the present study, consisted of verifying whether, as already shown in chicks (Tommasi et al. 1997; Tommasi and Vallortigara 2000), once the rats learned to localize the center of the enclosure, they could also transfer this spatial ability to enclosures differing in shape and/or in size.

The experiment was carried out at the Centre for Research in Cognitive Neuroscience, CNRS, Marseille, France. The subjects

were 12 male rats (Long Evans strain), weighing between 250 and 350 g at the moment of their arrival at the laboratory. The rats were handled daily during the week before the beginning of the experiment. During the same period, a restricted amount of food was made available to the animals in order to achieve a loss of weight corresponding to the 15% of the initial weight. This diet was maintained during the whole duration of the experiment to keep the rats in the necessary motivational state to make food attractive and actively searched.

The apparatus used to train the rats was a square-shaped enclosure, made with wooden walls (length 70 cm, height 40 cm). The enclosure was placed on the floor of an empty experimental room (350 × 200 cm). The floor of the enclosure was filled with a layer of sawdust (depth, 5 cm). The light in the room was provided by a central overhead fluorescent light (100 W).

The enclosures used for testing were also made with wooden walls (height, 40 cm) and they had the following shapes: rectangular-shaped enclosure (70 × 140 cm), double-side square-shaped enclosure (140 × 140 cm), and equilateral triangle-shaped enclosure (side, 140 cm).

At the beginning of training, a small food pellet was placed on the sawdust in the center of the enclosure. The rat was introduced to the enclosure and allowed to search the food for 1 min (a "trial"). In the first trial in a session, the task was very simple, as the food was directly accessible. Between trials, the rat was removed from the enclosure and a new food pellet was hidden in the center some millimeters under sawdust, deeper and deeper from trial to trial. By the last trial in a series of 10 (one session), the food was completely hidden under sawdust. Each rat received two daily training sessions. The aim of training was to reach a situation in which the rat searched precisely in the central position of the enclosure and dug to uncover (and eat) the food, relying only on its spatial memory. Some experimental precautions were taken in order to force rats to rely exclusively upon the geometry of the environment during orientation. Before each training session, the enclosure was displaced to a new position in the room to avoid distant landmarks being used instead of the shape of the enclosure. The apparatus could be easily moved along the two principal axes of the room, thus allowing the experimenter to place it in a random position over the room's surface, with the constraints that the enclosure was displaced at least 1 m and rotated at least 45°, thus assuring that there was no overlap between the old and the new area occupied by the enclosure between two consecutive sessions. Moreover, an interfer-

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Article and publication are at <http://www.learnmem.org/cgi/doi/10.1101/lm.60904>.

Figure 1 (Top squares in each row) Search trajectories of the 12 rats in the training enclosure. Each representation is obtained by superimposing the search trajectories recorded during five trials (trials 1–2, black; trials 3–5, gray). (Bottom squares in each row) Corresponding distribution of the average time spent by the same rats in the training enclosure during the five trials.

ence procedure was adopted to avoid rats being oriented by means of olfactory cues due to the presence of food; three food pellets were hidden in small metal cups under the sawdust at noncentral locations of the enclosure (allowing rats to perceive the smell of food without obtaining it). In fact, in the context of this daily training procedure, the rats also searched in the places where these inaccessible cups were located, and as it was impossible to reach the food, they searched more and more centrally. The three metal cups were placed at new locations before each session. Finally, at each trial, the rats were introduced to the enclosure at a different location and with a different body orientation, in order to exclude the use of motor strategies. The four corners were used as the releasing points, and a randomized sequence was used to determine which corner had to be used at any given trial. The orientation of the rat's sagittal body axis at release was chosen randomly among three possible orientations—facing the corner along the bisector, facing the corner and flanking the wall on the left side, or facing the corner and flanking the wall on the right side.

After 3 wk of training, the search behavior of the rats in the absence of food was recorded by means of a video camera fixed above the enclosure. The video camera could not be moved from its position on the ceiling, thus forcing the recording to take place with a standard position of the enclosure relative to the experimental room in terms of its absolute position and orientation. Before the recording started, the food cups were removed from the enclosure, and the sawdust was replaced in order to remove any olfactory trace. Each rat received a series of five consecutive recorded trials in the training enclosure (1 min each) with the same details of introduction (in terms of point of release and body orientation at release), as during training. Subsequently, the rats' spatial behavior was recorded during five consecutive test trials (1 min each) into each of the novel enclosures, randomizing the order of presentation of the three shapes for each rat. The test enclosure was positioned below the video camera, in the standard position. Between each series of recorded trials, the rats received a short retraining session (five trials) in the presence of food in the smaller square-shaped enclosure, to avoid extinction of search behavior. At each retraining session, the inaccessible food cups were placed again under the sawdust and the training enclosure was moved to a new position in the room.

The recording of the trajectories of rats in the enclosures, carried out by means of an automatic tracking system, allowed us to map the topography of spatial search of the animals. First, the five trajectories obtained during each rat's test trials were superimposed on each other. This graphic representation, when applied to the training enclosure shows that the rats searched precisely in the center of the environment (Fig. 1). Despite rats spending a large amount of time along the walls of the enclosure, a spatial behavior typical of rodents and known as 'thigmotaxis' (Schöne 1984; see also Eilam and Golani 1989 for a more detailed account of rats' exploratory modes of behavior), they performed rapid excursions back and forth to the central region of the enclosure, where they searched for the (absent) food by digging.

Figure 2 Overall distribution of the average time spent by all rats in the training enclosure during the five trials.

The spatial organization corresponding to these excursions can be appreciated graphically in the form of centripetal paths from the periphery of the enclosure toward its center, and centrifugal paths in the opposite direction.

The spatial coordinates associated with the individual trajectories were then automatically processed in order to reveal the overall topography of spatial search for each animal (Fig. 1) and for the whole group of animals (Fig. 2). Enclosures were subdivided into a number of bins, and the time spent in each bin by each rat (Fig. 1) and by all rats (Fig. 2) was averaged and linearly interpolated, thus obtaining gray level plots of the individual and global search-density distributions. These graphs represent the average amount of time spent by each rat and by all rats in the different zones of the enclosure during a test. It is possible to observe that for almost all individual animals as well as the group as a whole, the maximal intensity (excluding peaks along the periphery) is located in a small central patch.

The searching behavior in the rectangular-shaped test enclosure is again characterized by quick excursions toward the central region of the environment, analogous to those observed in the training enclosure, as it can be noticed in the graphs representing individual trajectories (Fig. 3), whereas the dwell time distributions (Figs. 3 and 4) make it easy to understand that almost all rats transferred what they had learned in the square-shaped enclosure to the novel shape, searching mostly in an elongated central patch.

Analogous results were obtained in the large square-shaped enclosure (Figs. 5 and 6) and in the equilateral triangle-shaped enclosure (Figs. 7 and 8). In these tests, once again, rats searched mostly in the regions of the enclosures corresponding to the geometric center. A slightly different result emerged only in the large square-shaped enclosure, in which a second peak can be observed (Fig. 6), due to a bimodal searching pattern adopted by some animals (see Fig. 5). This second peak is located in the center of one of the four quadrants composing the large enclosure, which has the same size as the training enclosure.

Figure 3 (Top rectangles in each row) Search trajectories of the 12 rats in the rectangular-shaped testing enclosure. Each drawing is obtained by superimposing the search trajectories recorded during five trials (trials 1-2, black; trials 3-5, gray). (Bottom rectangles in each row) Corresponding distribution of the average time spent by the same rats in the rectangular-shaped testing enclosure during the five trials.

Figure 4 Overall distribution of the average time spent by all rats in the rectangular-shaped testing enclosure during the five trials.

We believe that the distributions obtained in the training and test enclosures reflect the extent and precision of goal encoding and spatial generalization by rats, and we exclude that they may be the outcome of a spontaneous tendency to visit the central region of the various enclosures. This assumption is supported by recent research carried out in another rodent, the vole, *Microtus guentheri*, showing that in the spontaneous exploration of rectangular-shaped enclosures of sizes comparable with our enclosures, (1) voles travel most of the time in the periphery of the enclosures, and (2) the center is actively avoided (Eilam 2003; see also Eilam et al. 2003 for analogous results).

To further confirm the validity of the results obtained, statistical analyses were carried out on the quantitative data associated with the two-dimensional time distributions. The aim of these analyses was the comparison of the time actually spent in a central “test region”, with the time expected to be spent in the same region if the rats moved haphazardly in the enclosure (assuming a flat distribution of locomotor behavior over the entire surface of the enclosures). In the case of the training enclosure, a central square 18×18 cm was selected as the “test region” (6.6% of the total surface of the enclosure), and the average time spent by the rats in this region was computed as 17.49 sec, a much higher value than that expected assuming a flat distribution (4.04 sec; $t(11) = 4.97$, $P < 0.001$). The same computations and comparisons were performed for all of the test enclosures, and the results are reported in Table 1; rats spent a longer time in the central regions of all of the test enclosures as compared with what could be expected by a flat dwell-time distribution.

These results suggest that rats, whose spatial abilities were already known to depend on the geometric shape of the environment (Cheng 1986; Gallistel 1990; Pearce et al. 2001), can learn to localize the central position of an enclosure and transfer this learned ability to enclosures differing in shape and in size. It is important to emphasize that when the rats were transferred in the rectangular-shaped enclosure, the spatial distribution of searching stretched along the principal axis of the novel environment (and not simply as a result of averaging over the 12 individual distributions), although showing a clear and distinctive peak in the geometric center. When transferred in the enlarged square-shaped enclosure, the spatial distribution of search-

ing appeared accordingly enlarged, and a second peak emerged in the center of one of the composing quadrants, largely as a result of bimodal searching patterns of some rats. These results, if compared with data obtained using the same task in chicks (Tommasi et al. 1997; Tommasi and Vallortigara 2000), and using a similar task in pigeons (Spetch et al. 1997), suggest a stronger reliance on geometric cues in rats than in the avian species tested so far. In fact, when chicks were tested for transfer in novel enclosures after being trained in a square-shaped enclosure, their searching behavior turned out to be more influenced by the use of absolute distances from the walls of the enclosures, especially when these were much larger in size than the training enclosure (Tommasi et al. 1997; Tommasi and Vallortigara 2000). Similarly, pigeons trained to localize the central position inside an array of four landmarks arranged as a square, when tested for transfer in a stretched arrangement of the same array or in an enlarged version

of the array, searched mainly at locations matching the absolute distance from the landmarks in the training array (Spetch et al. 1997; see also Spetch et al. 2003). Analogous results were reported for another rodent species, the gerbil, in a study by Collett et al. (1986); in that case also, the searching behavior in transformed versions of a landmark-defined search space was strongly influenced by the use of absolute distances from individual landmarks. Thus, it seems that the differences obtained so far in rodents and birds can be accounted for on the basis of the different set-up used, rather than on differences between species (but see Jones et al. 2002 for discrepancies between avian species in a landmark-defined spatial bisection task). In general, when the search space is defined by an array of landmarks, the localization of the central position appears to be controlled by the distance and bearings obtained from individual landmarks. On the other hand, when the environment is defined by a number of surfaces arranged as a solid shape, the same task seems to depend more on the global geometry (see Gray et al. 2004 for recent evidence of pigeons' encoding of distance relations when searching for the center in an enclosed environment). Methodological differences are thus issues demanding prudence when comparing results obtained in different studies.

It is relevant to notice that when both geometry and landmarks could, in principle, control rats' spatial search in enclosed spaces, the former type of information seems always to play a major role, be it spatially segregated from landmark information (as in the case of Pearce et al. 2001, in which a local beacon was

Table 1. Comparison Between Observed and Expected Times Spent by Rats in a Central Region of the Enclosures

Enclosure	Time spent	Time expected	Student's <i>t</i> (DF = 11)
Square-shaped (training)	17.49 sec	4.04 sec	4.97 (***)
Rectangular	7.6 sec	2.02 sec	3.9 (***)
Large square-shaped	5.68 sec	1.01 sec	6.69 (****)
Triangular	9.48 sec	2.02 sec	9.48 (****)

Figure 5 (Top squares in each row) Search trajectories of the 12 rats in the large square-shaped testing enclosure. Each drawing is obtained by superimposing the search trajectories recorded during five trials (trials 1–2, black; trials 3–5, gray). (Bottom rectangles in each row) Corresponding distribution of the average time spent by the same rats in the large square-shaped testing enclosure during the five trials.

Figure 6 Overall distribution of the average time spent by all rats in the large square-shaped testing enclosure during the five trials.

present in the open space of a watermaze; see also Hayward et al. 2003 for related results) or somehow incorporating it (as in the case of Cheng 1986, in which distinctive panels were attached to the walls of a rectangular-shaped enclosure; see also Benhamou and Poucet 1998). Such a strong reliance on geometry in rats seems to support the results obtained in the present experiment.

Whether the learning abilities reported in all of these studies depend on the representation and use of abstract geometric rules, is a matter that would certainly benefit from further empirical research, but also from theoretical considerations about the existence and the nature of concepts in animals as inferred from experiments on generalization and discrimination abilities (see Lea 1984 for an analysis of the problem). However, it is of course not obvious that a spatial learning skill of the type that was investigated here must necessarily be considered in the frame of concept formation, as more basic mechanisms might be at work, such as the minimization of the differences between distances from two or more surfaces.

Electrophysiology research on hippocampal place cells (neurons whose activity depends on the spatial position of the rat in a given environment) showed that the major determinant of shape and location of a cell's place fields, when the firing rate of the cell is recorded while rats forage in enclosures differing in shape and size, seems to be the distance from two or more walls (O'Keefe and Burgess 1996). A strong resemblance between the spatial distributions of these place fields as recorded in a square-shaped and a rectangular-shaped enclosure, and the spa-

tial search distributions obtained in the analogous environments in the present study, seems to suggest that rats actually relied on the encoding of distances from the walls of the enclosure during the transfer tests. Moreover, it was shown recently that the place fields corresponding to two geometrically different enclosures progressively differentiate over time; after an initial stage of homotopy (during which the neuron fires in spatially corresponding regions of the two environments), the place cell starts to fire in unrelatable spatial regions of the two enclosures (Lever et al. 2002). Beside the fact that the hippocampus could play a relevant role in place navigation on the basis of environmental shape, as suggested by recent lesion evidence (A. McGregor, A. Hayward, J.M. Pearce, and M. Good, in prep.), it must be added that neurons in the subiculum and entorhinal cortex have been also reported to retain long-lasting homotopic place fields in geometrically different environments (Sharp 1997, 1999), thus providing more clues for the candidate neural structures as the basis of the spatial generalization that has been here reported.

ACKNOWLEDGMENTS

This research was supported by a Fondation Fyssen post-doctoral grant to L.T. during the years 2000–2001.

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Figure 7 (Top triangles in each row) Search trajectories of the 12 rats in the triangular-shaped testing enclosure. Each drawing is obtained by superimposing the search trajectories recorded during five trials (trials 1-2, black; trials 3-5, gray). (Bottom rectangles in each row) Corresponding distribution of the average time spent by the same rats in the triangular-shaped testing enclosure during the five trials.

Figure 8 Overall distribution of the average time spent by all rats in the triangular-shaped testing enclosure during the five trials.

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Received March 10, 2003; accepted in revised form January 7, 2004.

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Learn. Mem. 2004, **11**:

Access the most recent version at doi:[10.1101/lm.60904](https://doi.org/10.1101/lm.60904)

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