

# Effects of Spatial Food Distribution on Search Behavior in Rats (*Rattus norvegicus*)

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To analyze how search strategies are adapted according to the geometric distribution of food sources, the authors submitted rats to a search task in which they had to explore 9 food trays in an open field and avoid visiting already-depleted trays. Trays were spatially arranged in 4 independent configurations: a cross, a  $3 \times 3$  matrix, 3 clusters of 3 trays each, and a random configuration. Rats exhibited differential search efficiency as a specific effect of the susceptibility of the configurations to being explored in a principled way: Crosses were first, matrices or clusters were in the middle, and random configurations were last. Although no exhaustive searches or highly principled patterns were observed in any of the configurations, performances improved as the sessions went by. Thus, structural affordances of the environment influence the construction not only of search strategies but also of information linked to where the reward is.

*Keywords:* search patterns, spatial cognition, clusters, navigation

Rats' search abilities have been extensively analyzed in spatial tasks such as differently baited radial mazes (Olton & Samuelson, 1976), the Morris water maze (Morris, Garrud, Rawlins, & O'Keefe, 1982) or the open field (Denenberg, 1969). Although in mazes such as the Morris water maze and the open field there are no predefined trajectories to follow and thus these tasks are performed in an unconstrained way, in mazes such as the radial maze the arms provide a preset number of alternative routes and thus constrain search behavior.

It has been demonstrated that rats are able to take into account the physical constraints of the differently shaped mazes (Schenk, Contant, & Grobety, 1990). Roberts and coworkers (Macuda & Roberts, 1995; Phelps & Roberts, 1989; Roberts, 1979, 1984; Roberts & Ilerish, 1989) showed that when the spatial structure of the radial maze supported a hierarchical search organization, search efficiency strikingly increased. Moreover, Dallal and Meck (1990) showed that rats took into account different visual cues to visit radial arms in clusters and to visit them one after the other. More recently, in a full-baited 10-session radial maze paradigm, Mandolesi, Leggio, Graziano, Neri, and Petrosini (2001) demon-

strated that rats modified exploratory strategies by increasing the number of visits to adjacent arms as the sessions went by. They also demonstrated that in an open field containing several objects rats were able to change their search strategies according to the spatial arrangement of the objects (Mandolesi, Leggio, Spirito, & Petrosini, 2003), indicating that physical constraints may modify the means of spatial exploration. In hierarchically baited radial mazes, the rats' clustered choices are considered to reflect a chunking process similar to that used by humans to enhance information retrieval. Typically, rats enter the arms in a given set before they have sampled all the arms in another one. Thus, they do not appear very accurate on hierarchically structured tasks, at least in mazes such as the radial maze, that do not allow unconstrained search behavior.

To study search patterns in animals, recent studies (Brown & Terrinoni, 1996; Brown & Winterstein, 2004; Brown, Zeiler, & John, 2001; De Lillo, 1996; De Lillo, Aversano, Tuci, & Visalberghi, 1998; De Lillo & McGonigle, 1997; De Lillo, Visalberghi, & Aversano, 1997; Valsecchi, Bartolomucci, Aversano, & Visalberghi, 2000) introduced new spatial tasks in which the structural affordances of the search space were manipulated to make animals' cognitive strategies emerge. These studies demonstrated that animals explore different arrays of food resources with progressively improved efficiency, reducing repeated visits to already-depleted items as trials went by (Brown & Terrinoni, 1996; Brown & Winterstein, 2004; Brown, Zeiler, & John, 2001; Di Gello, Brown, & Affuso, 2002; Greene & Cook, 1997). In capuchin monkeys (*Cebus apella*), search efficiency differed depending on spatial constraints and was higher in search spaces that could be organized in spatial chunks (clustered or linear arrangements). Furthermore, monkeys' search behaviors are characterized by principled strategies such as choosing fixed starting and ending points

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and main travel directions in search bouts (De Lillo et al., 1998; De Lillo et al., 1997). Conversely, mice (*Mus Musculus domesticus*) are more efficient with the matrix than with the cluster configuration and do not develop any evident search strategy (Valsecchi et al., 2000).

The notion that rats' behavior in the radial maze is guided by optimization principles cannot be positively extended to multiple-reward open fields, similar to those developed by De Lillo et al., (1997), simply on the basis of environmental constraints. The aim of the present study was to evaluate the effects elicited by the spatial configurations of nine food sources on rats' search patterns in conditions in which the rats had to keep track of the visits made over time in the absence of constrained trajectories to travel and of physical traces left from choices they had already made. In particular, our objective in this study was to analyze whether search space is explored in a principled manner, based on the spatial relationships of the configuration of food sources, and to identify the occurrence of chunking patterns as a means of reducing data in a task that made demands on the memory system.

Rats (*Rattus norvegicus*) were tested in four different food arrays. In the first three spatial configurations, the nine trays containing rewards were organized in regular compositions: cross, matrix, or cluster configurations (De Lillo et al., 1998; De Lillo et al., 1997). In the fourth one, food trays were placed without any particular geometrical arrangement (random configuration). However, note that all random configurations do not necessarily imply the absence of spatial constraints. In fact, random configurations also can feature, at least in some of their parts, subgroups defined by spatial proximity or almost linear arrangements of items. Taking this into account, the present random configuration was arranged so that the spatial constraints (lines, geometrical shapes) did not involve more than three trays.

## Method

### Subjects

Twenty adult male Wistar rats (*Rattus norvegicus*), weighing 200–250 g at the beginning of testing, were used in this experiment. The rats were housed 2 rats to a cage (42 × 26 × 18 cm) furnished with wood shaving bedding and kept on a standardized light–dark schedule (12:12 hr; lights on at 0700 hours). The room temperature was 21 °C and the relative humidity 60% ± 5%. Three days before the experiment, the rats were placed on food deprivation with free access to water. They were reduced to 90% of ad lib weight by scheduled feeding (30 min of free feeding every day) and were maintained at this level throughout the experiment by being given a restricted amount of food (Mucedola 4RS21 standard diet GLP complete feed for mice and rats; Mucedola, Milan, Italy) each day. The rats were weighed once a day. The food deprivation lasted 8 days. During this period, the rats showed no signs of aggression during or between feeding times and no signs of distress. The rats' behavior in their cages was monitored twice a day.

All experiments were carried out according to the European Community Council Directives of November 24, 1986 (86/ 609/ EEC) and approved by the Ethical Committee on animal experiments of University of Rome "La Sapienza". Rats were randomly assigned to one of the four different groups, each of which included 5 rats, according to the different tray arrangement.

### Apparatus

The apparatus was placed in a lab that was dimly and uniformly illuminated by a masked neon ceiling lamp. It consisted of a round plywood table (150 cm in diameter, 2.5 cm thick) raised 50 cm from the floor by a rotating support. There was a 50-cm grey opaque wall around the table. The wall greatly reduced the number of external cues in the arena. However, use of spatial cues from the ceiling could not be prevented because there was no cover over the arena. Nine blue chemically inert tube caps (3 cm in diameter, 2 cm deep) used as food trays were arranged according to the spatial configurations described in the *Procedures* section. The depth of the tray prevented the rats from seeing the reward at a distance but allowed for an easy reward, that is, eating. The reward was a single piece of the previously described standard food for rats sweetened by condensed milk (Nestlé Italiana, Milan, Italy).

### Pretraining

Before the experiment began, the rats were submitted to a 3-day pretraining. On the 1st day, the rats were manipulated for 10 min in their home cages, which had been placed in the experimental lab, to become accustomed to the experimenters and the lab environment. On the 2nd day, pairs of rats were allowed to explore the table freely for 15 min, and three baited food trays were randomly arranged on the table. On the last day of training, individual rats were again placed on the table with three baited trays and allowed to explore it for 15 min. During the 2nd and 3rd days of pretraining, the rats visited the food trays and emptied their contents during the 15 min of exploration. Testing sessions began the next day.

### Procedures

Spatial configurations were derived from preceding studies (De Lillo et al., 1998; De Lillo et al., 1997; Valsecchi et al., 2000; Figure 1). In the cross configuration, the trays were arranged in an X formation in the center of the table, with trays 25 cm apart. In the matrix configuration, the food trays were arranged in a 3 × 3 square matrix in the center of the table, with trays 25 cm apart. In the cluster configuration, the trays were arranged in triplets 120° away from each other, with the center of each triplet placed 40 cm away from the center of the table and with trays placed 25 cm apart. In the random configuration, trays were randomly arranged on the table and were kept in this arrangement in every trial. Care was taken to avoid putting two adjacent trays less than 25 cm apart and to avoid that the arrangement featured subgroups defined by spatial proximity, by almost linear arrangements of items, or by any obvious (e.g., triangular, squared) geometrical arrangement of items.

The table was cleaned at the end of each trial, but the trays were not. Instead, a new piece of food was added to provide a constant odor gradient and to prevent the rats from sniffing the presence of the reward far away from the tray. Table and trays were cleaned at the end of each session.

In each trial, the goal was to collect all nine rewards, which were never replaced during the trials. At the end of each trial, the rats were put back in their cages for 15 min. Each rat underwent six trials per session, one session a day for 5 consecutive days.

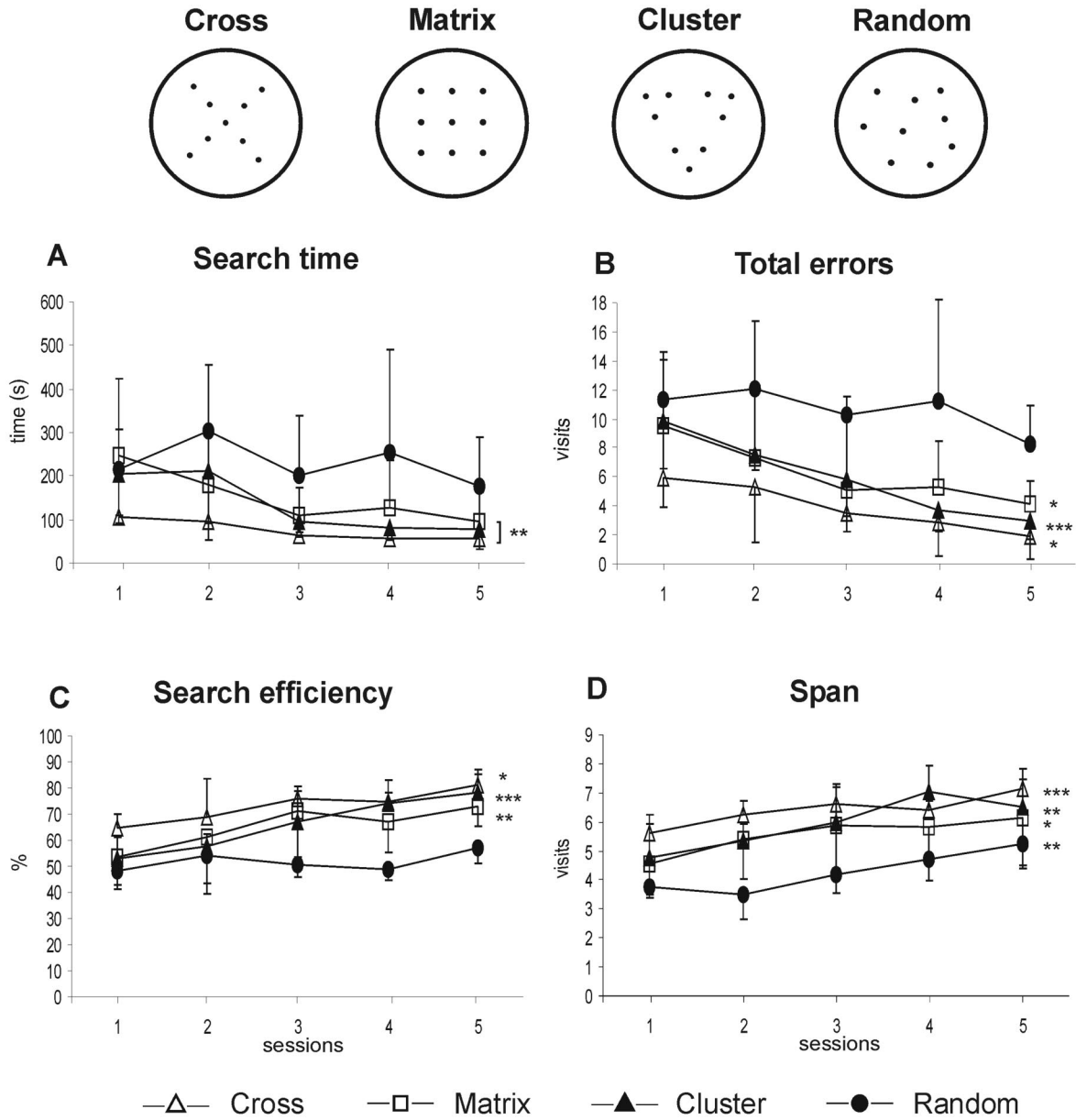


Figure 1. Performances displayed by rats across the five sessions of the search task in cross, matrix, cluster, and random configurations. Tray arrangement in the four configurations is depicted at the top of the figure. A: Mean ( $\pm$  confidence interval [CI]) search time used to complete the task. B: Mean ( $\pm$  CI) total errors. C: Mean percentage ( $\pm$  CI) of correct visits on the total visits (search efficiency). D: Mean ( $\pm$  CI) longest sequence of correct visits (span). The asterisks at the end of the lines indicate the significance level of the respective one-way analyses of variance. \*  $p < .05$ ; \*\*  $p < .001$ ; \*\*\*  $p < .0001$ .

At the beginning of the trial, the rat was placed on the table facing the center at one of the starting points defined by the cardinal points (N, S, W, or E) in cross, matrix, and random configurations, and at one of three starting points (N, SW, or SE) in the cluster configuration. Starting points were balanced across trials. To further reduce spatial encoding of the food source position based on external cues, at the beginning of each trial the table was rotated to one of four different positions (N, S, W, or E) in the cross, matrix, and random configurations, and to one of three different positions (N, SW, or SE) in the cluster configuration, in a counterbalanced order.

To analyze whether the reward odor from the food trays could guide search behavior, we conducted a nonreinforced probe trial as the seventh trial after the six trials of the last session of the random configuration. In this probe trial, food trays were carefully washed and left empty.

*Behavioral Parameters*

Rats were allowed to freely explore the apparatus. Each trial was videotaped to permit off-line analyses. A trial ended when all nine rewards had been collected, 30 choices had been made, or 15 min

had elapsed. A visit was defined as nose poking or touching a food tray to sniff it. Because the food trays were never rebaited, an optimal performance consisted of visiting all nine trays only once.

In each of the six trials of a session, the following parameters were analyzed: (a) *search time*, the time (in s) used to complete the trial by collecting all nine rewards, by performing 30 visits, or by consuming 15 min; (b) *total errors* performed in a trial (considering either revisits and no visits to a tray so that it remained baited); (c) *search efficiency*, the percentage of correct visits out of total visits; and (d) *span*, defined as the longest sequence of correct visits. Also, the distance (in cm) traveled on the table and the distance traveled in exploring a peripheral annulus with a 20-cm radius were calculated. The kind of trajectory, direct or indirect, used to reach a tray, either correct or incorrect, was also analyzed. The trajectory was considered direct when the distance traveled by the rats to reach a new tray exceeded the most direct between-tray distance by no more than 10%.

In the cluster configuration, other parameters were analyzed: (a) number of clusters visited or revisited in each trial (this parameter ranged from the worst value of 30 to the best value of 3) and (b) number of clusters depleted with three correct visits performed one after the other (this parameter ranged from the worst value of 0 to the best value of 3). The errors were classified as *within-cluster errors*, that is, the revisits to a tray belonging to the same cluster the rat was visiting, or *across-cluster errors*, that is, the late revisits to a tray belonging to an already-visited cluster in that trial. The across-cluster errors were further divided into revisits to a tray belonging to an already-completed cluster and revisits to a tray belonging to a previously visited but not completed cluster.

*Statistical Analysis*

Metric unit results of rats belonging to the different experimental groups were compared with one-, two-, or three-way analyses of variance (ANOVAs), followed by post hoc multiple comparisons using Duncan’s test. Correlation between data was also tested by means of Pearson’s *r*.

**Results**

*Parameters*

*Search time.* The time needed to complete the task was similar in the cross, matrix, and cluster configurations, whereas it was significantly longer in the random (Figure 1A) configuration. The

corresponding two-way ANOVA and the post hoc comparisons are shown in Table 1.

*Total errors.* The nine trays were visited equally in all configurations, as indicated by ANOVAs on the nine positions, which revealed no significant difference among trays in any configuration: cross,  $F(8, 36) = 0.28, p = ns$ ; cluster,  $F(8, 36) = 0.58, p = ns$ ; matrix,  $F(8, 36) = 0.02, p = ns$ ; random,  $F(8, 36) = 0.12, p = ns$ . When the total errors (revisits and no visits) were taken into account, a clear among-group difference was evident, with the highest number of errors made in the random configuration (Figure 1B). The corresponding two-way ANOVA and the post hoc comparisons are shown in Table 1.

When the percentage of no visits was separately analyzed, very low values (about 0.05%) were found in all configurations, but the random configuration displayed a value of about 4%. The corresponding two-way ANOVA and the post hoc comparisons are shown in Table 1.

To verify the possible modifications of intrasession performances, we compared the number of errors made in the first and sixth trial of each session in the four spatial configurations. A clear decrease in errors was present in almost all configurations in almost all sessions, as demonstrated by a three-way ANOVA (Configuration  $\times$  Trial  $\times$  Session) that revealed highly significant configuration,  $F(3, 16) = 7.49, p < .005$ ; trial,  $F(1, 16) = 20.16, p < .0005$ ; and session,  $F(4, 64) = 2.67, p < .05$ , effects. Between-factor and among-factor interactions were not significant: Configuration  $\times$  Trial,  $F(3, 16) = 0.72, p = ns$ ; Configuration  $\times$  Session,  $F(12, 64) = 0.48, p = ns$ ; Trial  $\times$  Session,  $F(4, 64) = 0.96, p = ns$ ; among-factor interaction,  $F(12, 64) = 0.72, p = ns$ .

Note that in the first trial of all sessions the rats generally displayed a higher number of errors than in the sixth trial of the preceding session. However, considering the task as a whole, significant improvement was present over the course of the sessions in all configurations except for the random configuration, in which statistical significance was not reached.

*Search efficiency.* The rats never attained the most efficient performance in absolute terms because the number of visits to exhaustively conclude the trial was never near nine, that is, a value that indicated 90%–100% search efficiency, in any spatial configuration. Namely, in the cross configuration, the number of visits in the last session was 11.33 (confidence interval [CI] =  $\pm 0.72$ ), with a search efficiency of 81% (Figure 1C). In the cluster and matrix configurations, the number of visits was 11.93 (CI =

Table 1  
*Statistical Comparisons (Two-Way ANOVAs and Duncan’s Tests) of Behavioral Responses in the Four Spatial Arrangements*

Parameter	Configuration effect		Session effect		Interaction		Duncan’s test					
	F value (df = 3, 16)	p	F value (df = 4, 64)	p	F value (df = 12, 64)	p	M vs. C	M vs. R	M vs. Cr	C vs. R	C vs. Cr	R vs. Cr
Search time	7.00	<.005	7.72	<.0001	1.18	ns	ns	<.05	ns	<.05	ns	<.005
Total errors	10.10	<.005	18.06	<.0001	1.20	ns	ns	<.005	ns	<.005	ns	<.0005
No visits	3.41	<.05	2.53	<.05	2.56	<.05	ns	<.05	ns	<.05	ns	<.05
Search efficiency	9.62	<.001	21.4	<.0001	2.23	<.01	ns	<.005	ns	<.005	ns	<.0005
Span	14.59	<.0001	20.86	<.0001	1.45	ns	ns	<.005	<.05	<.0005	ns	<.0005
Traveling distances	3.42	<.05	19.19	<.00001	0.97	ns	<.05	ns	<.05	ns	ns	ns
Peripheral sectors	3.71	<.05	25.66	<.00001	3.51	<.005	ns	ns	<.05	ns	<.05	ns

Note. M = matrix configuration; C = cluster configuration; R = random configuration; Cr = cross configuration.

$\pm 0.97$ ) and 13.07 (CI =  $\pm 1.28$ ), with a search efficiency of 78% and 73%, respectively (Figure 1C). In the random configuration, the number of visits in the last session was 17.17 (CI =  $\pm 2.03$ ), with a search efficiency of 57% (Figure 1C). The corresponding two-way ANOVA and the post hoc comparisons are shown in Table 1.

**Span.** The longest sequence of correct visits performed in each trial represented a measure of the item span. The best performance was exhibited in the cross configuration ( $\bar{X}$ : 7.13; CI =  $\pm 0.27$ ) followed by the cluster ( $\bar{X}$ : 6.50; CI =  $\pm 1.07$ ), and the matrix ( $\bar{X}$ : 6.17; CI =  $\pm 1.36$ ) configurations, and finally by the random configuration, in which the worst performance was made ( $\bar{X}$ : 5.23; CI =  $\pm 0.66$ ). The corresponding two-way ANOVA and the post hoc comparisons are shown in Table 1.

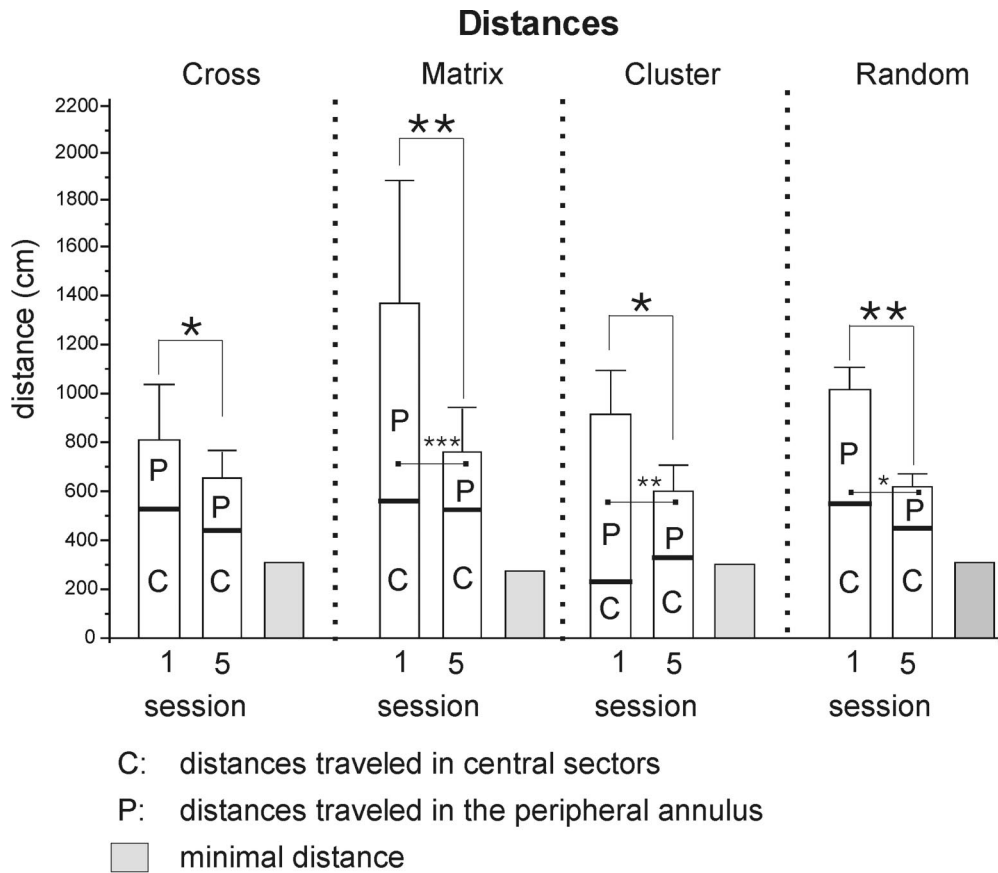
**Traveling distances.** The total distance traveled to pick up the rewards was significantly influenced by the spatial configuration of the search space. The rats traveled the longest distance in the matrix configuration. In all configurations, the distance traveled by the rats was reduced as the sessions went by; however, they never reached the minimal distance needed to visit all nine trays in any of the configurations (Figure 2). The corresponding two-way ANOVA and the post hoc comparisons are shown in Table 1.

Then we analyzed travel in the peripheral sectors. The corresponding two-way ANOVA and the post hoc comparisons are

shown in Table 1. Note that in the first session of the matrix configuration the rats traveled most in the peripheral annulus (peripheral vs. central sectors:  $p < .05$ ). This behavior was significantly reduced in the last session (first-session peripheral sector vs. fifth-session peripheral sector:  $p < .0001$ ). A similar pattern was displayed in the cluster configuration but with lower values because in the first session the rats tended to remain outside the configuration before moving into it (peripheral vs. central sectors:  $p < .0001$ ). Also in this configuration, this behavior was significantly reduced in the last session (first-session peripheral sector vs. fifth-session peripheral sector:  $p < .001$ ). At the end of the testing, the rats traveled mainly in the central areas of the arena in all configurations.

**Exploration Rules**

To detail the explorative rules applied in picking up the rewards, we took into consideration whether the first tray visited was the one closest to the starting point or whether there was a preferred starting tray in each configuration regardless of the starting point. A three-way ANOVA (Closeness  $\times$  Session  $\times$  Configuration) revealed a significant closeness effect:  $F(1, 4) = 1772.3$ ,  $p < .00001$ ; whereas session effects,  $F(4, 16) = 1.0$ ,  $p = ns$ ; and configuration effects,  $F(3, 12) = 0.18$ ,  $p = ns$ , were not signifi-



*Figure 2.* Distances traveled in the first and fifth sessions in the four configurations. In each column, the respective distances traveled in the peripheral annulus (P) and in the central sector (C) are indicated. The minimal paths needed to perform the task are also depicted. \*  $p < .05$ ; \*\*  $p < .001$ .



cant. The among-factor interaction was also significant,  $F(12, 48) = 4.01, p < .0002$ .

We also analyzed whether a tray (correct or incorrect) was reached through direct or indirect trajectories. A three-way ANOVA (Configuration  $\times$  Session  $\times$  Trajectory) revealed significant session,  $F(4, 64) = 2.98, p < .05$ ; and trajectory,  $F(1, 16) = 121.67, p < .0001$ , effects; whereas the configuration effect was not significant,  $F(3, 16) = 3.02, p = ns$ . Between- and among-factor interactions were also significant: Configuration  $\times$  Session,  $F(12, 64) = 2.67, p < .005$ ; Configuration  $\times$  Trajectory,  $F(3, 16) = 5.10, p < .05$ ; Session  $\times$  Trajectory,  $F(4, 64) = 26.34, p < .0001$ ; and among-factor interaction,  $F(12, 64) = 4.68, p < .0001$ .

Successively, we analyzed the kind of trajectory used in reaching a new tray by distinguishing whether it was correct (Figures 3A and 3C) or incorrect (Figures 3B and 3D). A three-way ANOVA (Configuration  $\times$  Trajectory  $\times$  Correctness) revealed significant configuration,  $F(3, 16) = 3.32, p < .05$ ; trajectory,  $F(1, 16) = 126.6, p < .0001$ ; and correctness,  $F(1, 16) = 59.9, p < .0001$ , effects. All between- and among-factor interactions were significant: Configuration  $\times$  Trajec-

tory,  $F(3, 16) = 4.98, p < .05$ ; Configuration  $\times$  Correctness,  $F(3, 16) = 12.61, p < .0005$ ; Trajectory  $\times$  Correctness,  $F(1, 16) = 692.32, p < .0001$ ; and among-factor interaction,  $F(3, 16) = 23.37, p < .0001$ . As shown in Figure 3A, in all configurations most visits to correct trays were made through direct trajectories (in the final session the percentage ranged from 70% in the cross configuration to 50% in the random configuration), whereas the least frequent response was a visit to a correct tray through an indirect trajectory (in the final session, the percentage ranged from 4% in the cross configuration to 10% in the cluster configuration; Figure 3C). Incorrect trays were more frequently reached through indirect trajectories in all configurations (Figure 3D) except for the random configuration, in which incorrect as well as correct trays were frequently reached through direct trajectories (Figure 3A and 3B).

*Search Strategies in Cluster Configuration*

In a configuration displaying closely grouped rewards, such as the cluster configuration, rats should complete each cluster

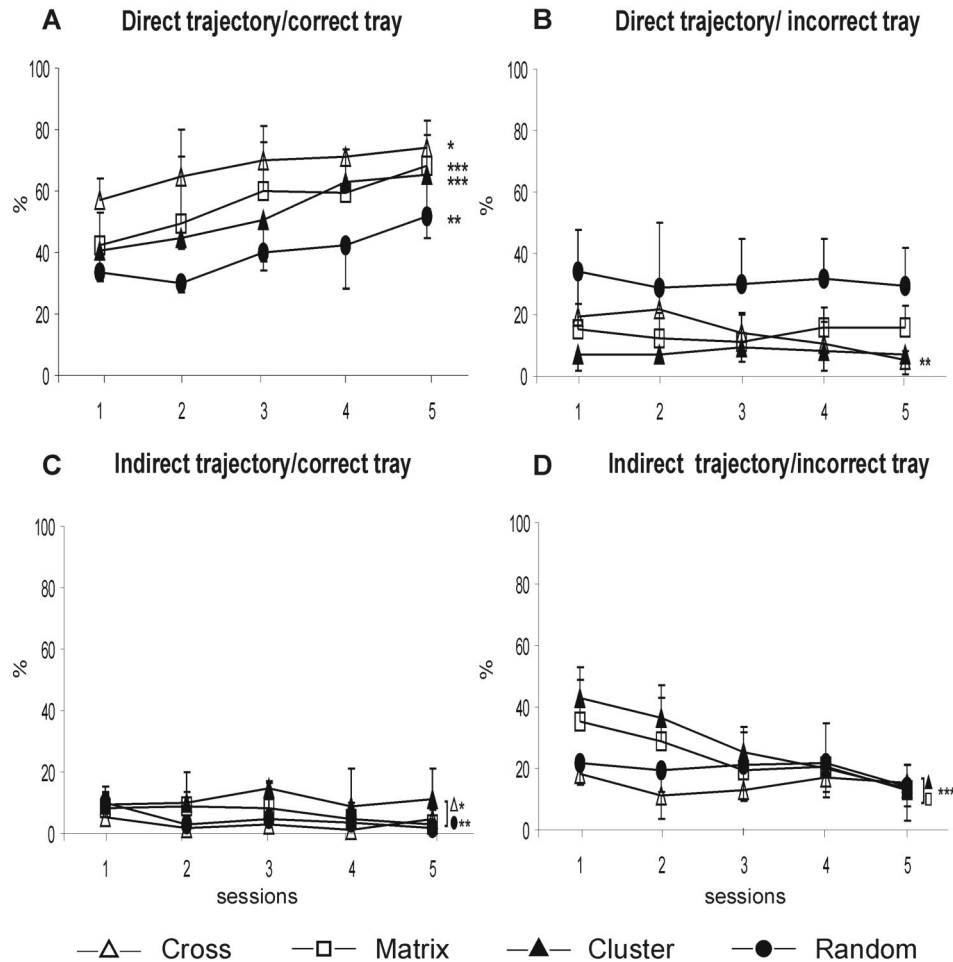


Figure 3. Performances displayed by rats across the five sessions of the search task in cross, matrix, cluster, and random configurations. A: Mean percentage ( $\pm$  confidence interval [CI]) of correct trays visited through a direct trajectory. B: Mean percentage ( $\pm$  CI) of incorrect trays visited through a direct trajectory. C: Mean percentage ( $\pm$  CI) of correct trays visited through an indirect trajectory. D: Mean percentage ( $\pm$  CI) of incorrect trays visited through an indirect trajectory. The asterisks at the end of the lines indicate the significance level of the respective one-way analyses of variance. \*  $p < .05$ ; \*\*  $p < .001$ ; \*\*\*  $p < .0001$ .

before moving on to the next one. In this way, they have only three items to remember at a time (the three trays within a cluster) and the position of the three clusters. Additional parameters were considered to analyze whether the rats used the spatial constraints afforded by the clustered space in this principled manner. Both the number of clusters visited in each trial (Figure 4A) and the number of clusters visited with three correct visits made one after the other (Figure 4B) were taken into account. The significant curves present in both parameters as the sessions went by indicated progressive tuning of the search strategies. We also analyzed whether the errors were within- or across-clusters and whether the across-cluster errors were late revisits to an already-completed cluster or to an uncompleted one. As shown in Figure 4C, the most frequent errors were revisits to a tray belonging to an already-completed

cluster. These were followed by revisits to a tray belonging to an uncompleted cluster and, finally, by within-cluster errors. A two-way ANOVA (Error  $\times$  Session) revealed a highly significant error effect:  $F(2, 12) = 10.27, p < .005$ . The effects of session,  $F(4, 48) = 0.32, p = ns$ ; and interaction,  $F(8, 48) = 1.36, p = ns$ , were not significant.

The existence of a relationship between the use of principled search and the ability to remember the already-visited sites was further supported by an analysis of the relationship between the frequency of late revisits and the frequency of exits from a cluster not fully depleted. When this correlation was analyzed, a high parallelism between measures emerged (Pearson's  $r = .94$ ). Good parallelism between measures also emerged (Pearson's  $r = .74$ ) when frequency of late revisits and frequency of completely depleted clusters were correlated.

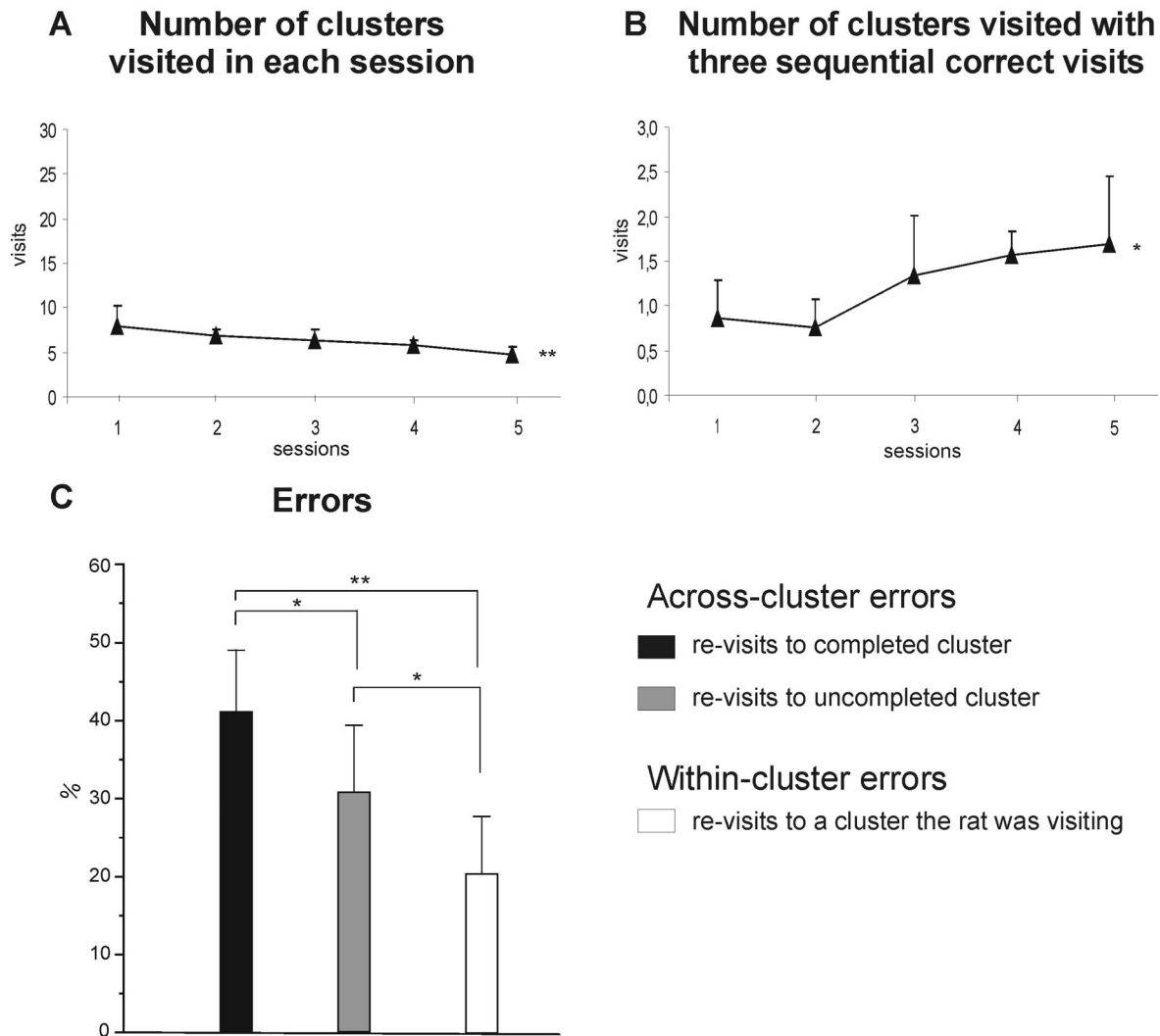


Figure 4. Performances in cluster configuration. A: Mean ( $\pm$  confidence interval [CI]) number of clusters visited or revisited in each session. B: Mean ( $\pm$  CI) number of clusters depleted with three sequential correct visits (performed one after the other). C: Mean percentage ( $\pm$  CI) of across- and within-cluster errors. In A and B, the asterisks at the end of the lines indicate the significance level of the respective one-way analyses of variance, whereas in C they indicate the significance level of the post hoc comparisons between kinds of errors. \*  $p < .05$ ; \*\*  $p < .001$ .

### Probe Trial

In the random configuration, the number of errors made in a nonreinforced probe trial ( $\bar{X} = 9.0$ ;  $CI = \pm 6.27$ ) was compared with the number of errors made in the sixth trial of the last session ( $\bar{X} = 15.4$ ;  $CI = \pm 10.73$ ). A one-way ANOVA showed no significant effect,  $F(1, 8) = 2.04$ ,  $p = ns$ . This finding indicated that performances were comparable in reinforced and nonreinforced trials, thus excluding that the odor traces of the reward guided the rats to baited trays or away from depleted ones.

### Discussion

The present research addresses the issue of the influence of spatial food distribution (De Lillo et al., 1997; De Lillo et al., 1998) on search behavior in rodents. The rats' performances improved in all configurations used and for almost all parameters considered in conditions in which they had to keep track of the trays already visited. They did this either by developing principled search strategies or by building long-term memory traces. Given the almost complete absence of extramaze (allothetic) cues, intramaze and idiothetic cues were used to learn the task. The intramaze cues were derived from the spatial relationships specified by the food trays themselves. The idiothetic cues were derived from the rats' own movements. They encompassed internal self-motion information provided by the vestibular, proprioceptive, and somatosensory systems; efference copies of motor commands; and external motion-related information such as optic flow (Biegler, 2000; Buzsaki, 2005; Etienne, Maurer, & Séguinot, 1996; Parron & Save, 2004; Paz-Villagran, Save, & Poucet, 2006).

An intrasession improvement in performance was present in exploring the different spatial distributions of rewards. This finding ruled out any interference effect among the trials in a session and, conversely, supported the presence of an intrasession ameliorative effect based on short-term memory traces. Furthermore, a clear intersession ameliorative effect was present in all configurations that maximized the amount of rewards depleted and minimized travel and time spent.

General observations included the following: The trajectories across the search space were irregular in all configurations; the preferred starting trays were those that coincided with the locations closest to the release site; all trays were visited equally; and highly principled patterns of searching could not be detected, even in the very last trials. The only strategy adopted by the rats was the "adjacency strategy" involving spatial search from one tray to the next, an adaptive behavior to explore a new environment (Timberlake, Leffel, & Hoffman, 1999). It is worth remembering that in exploring radial mazes with large center platforms animals tend to go to the adjacent arms; however, variability across species is reported in the literature (Hoffman, Timberlake, Leffel, & Gont, 1999; Timberlake & White, 1990; Timberlake & Hoffman, 2002). This adjacency strategy increases in frequency as the sessions go by, given its essential economy (Mandolesi et al., 2001).

However, the different spatial distribution of rewards produced marked differences on the rats' search behavior, as previously reported (De Lillo et al., 1998; De Lillo et al., 1997; Roche & Timberlake, 1998). The best performances were observed in the cross configuration and the worst in the random configuration. Performances in exploring the cluster and matrix configurations fell between the other two. This general behavior could be explained on the basis of the

number of trays within 25 cm of each other. The more trays (cross configuration), the more efficient were the rats, the fewer (random configuration), the less efficient.

### Exploration of Cross Configuration

In the cross configuration, the rats depleted the highest number of trays with the least amount of travel and in the least amount of time. This result indicates that the configurations the rats dealt with most efficiently were those with strong spatial constraints, such as the cross. To fully deplete the cross, the rat could use an end-to-end search pattern twice, moving along the lines and visiting adjacent trays. In fact, because of the linear configurations of loci as well as the practicability of moves to adjacent trays, they did not have to memorize the locations already visited. The trajectory adopted to explore a cross can work as a notational system that aids the use of a principled pattern and thus strongly reduces the memory load. However, to exhaustively deplete trays located in straight lines, a firm directional principle that prevents the inversion of the travel direction should be present. Conversely, the rats displayed occasional "unmotivated" travel inversions that provoked revisits and lowered the search efficiency to a good but not optimal value of 81%.

In conclusion, the results obtained in the cross configuration indicated the rats' capacity to make strategic use of the spatial structure of the search space. Thus, the rats should have performed better in the highly structured configuration than in the diffuse search spaces. On the other hand, the rats did not succeed in exhaustively depleting all trays because they lacked a rigorous directional principle.

### Exploration of Cluster Configuration

As demonstrated in monkeys, search efficiency is best expressed in a space that can be organized in clusters or spatial chunks (De Lillo et al., 1998; De Lillo et al., 1997). The chunking theory predicts that once the chunks have been retrieved the burden on memory should be lightened from the total number of places to be explored (in this case, nine) to the number of clusters constituting the search space (in this case, three). Thus, the hierarchical organization of memory afforded by chunking substantially reduces the working memory load and promotes higher level performances (Cohen, Pardy, Solway, & Graham, 2003; Macuda & Roberts, 1995; Terrace & McGonigle, 1994). Nevertheless, only the exhaustive depletion of a cluster before moving on to the next one collapses errors. Conversely, in the present paradigm chunking appears to be a strategy of relative strength, as indicated by studying the rats' performances as a function of the angular relationships among the arms of a radial maze (Schenk, Contant, & Grobety, 1990). In fact, the rats did not exploit the whole cluster before moving to the next one and returned to a cluster they had already visited more than once, visiting the already-depleted trays instead of exhausting the still uncompleted cluster. This behavior resulted in a rather high number of errors. Most errors were across-cluster and few errors were within-cluster. In other words, the rats found it more difficult to identify whole, not-yet-depleted clusters and less difficult to remember the trays visited within a cluster. Note that these two competencies are based on memory functions acting on different time courses. Even when monkeys searched in a patchy space, they made most of their errors in revisiting already-depleted clusters and made only a few within-



cluster errors (De Lillo et al., 1997). The relationship between organization of search and performance was also evident in the highly significant correlation between measures, a finding that indicated difficulty in keeping track of locations when the hierarchical organization of the search was weakened. It also showed the tendency of rats to visit farther trays, a tendency interpreted by Lachman (1965) as an innate preference for a change of stimulus. In a complex situation, such as the nine clustered trays, the compelling tendency to move away induced, on one hand, foraging behavior that prevented neglecting some trays and provoked, on the other, across-cluster revisits.

### *Exploration of Matrix Configuration*

Although the rats performed well in the matrix configuration, they did not carry out highly principled search patterns along rows or columns. In the absence of a structured search pattern, a reasonable strategy for performing accurately in the matrix configuration could be a compromise between visiting trays farther away than the previously visited one, a behavior promoting a good search between rewarded trays, and visiting the nearest one, limiting thus the information to be stored. Rats explored the matrix by alternating these two opposite patterns.

### *Exploration of Random Configuration*

When the spatial distribution of rewards was randomized, the rats exhibited the poorest performance level in this configuration on almost all parameters, suggesting their fine sensitivity to some major (linear, squared) geometrical cues that were almost absent in the random array of trays and present in the other configurations. It is interesting to note that some parameters such as search time, errors, and search efficiency displayed the lowest starting values, and their evolution failed to reach statistical significance. This finding indicates that the rats failed to learn explorative competencies when the spatial configuration of reward sources prevented spatial chunking (even if it is not completely effective in rats) or the use of the search space as a notational system. The irregular spatial arrangement of the rewards challenged any ordered strategy and prevented any strategic use of the spatial structure of the search space (Lachman, 1965; Olton, 1979). Probably, in the presence of reduced (if any) use of searching strategies, the rats could have acquired higher performance levels by exploiting their spatial memory competence. Evidently, this alternative required a memory load that was too heavy and, therefore, the rats' performances collapsed.

### *Trajectory Directness and Visit Correctness*

In almost all configurations, the rats tended to reach a never-before-visited tray through a direct trajectory and to reach an already-visited tray through a tortuous pathway. The close correlation between trajectory direction and tray correctness is a sign that the rats reach a tray without any hesitation when they are able to predict that the tray they are going to visit has not yet been depleted. Uncertainty about the correctness of a visit was reflected in insecurity about the trajectory. A comparable approach is widely used in analyzing rats' performances in the Morris water maze. By calculating heading angles from the starting point to the platform, it is possible to deduce whether the rat already knows where the

platform is when it detaches from the pool walls. The more precise the localizatory competence is, the more reduced the heading angle (Morris et al., 1982; Petrosini, Molinari, & Dell'Anna, 1996). Similarly, the trajectory to reach a tray indicates competence in the correctness of the visit the rat is going to make. The more robust the knowledge about the correctness of the tray is, the more direct the trajectory to reach it. Of interest, the rats tended to reach both correct and incorrect trays through direct trajectories only in the random configuration. Evidently, in the latter configuration the rats were unable to predict whether the tray they were going to explore had or had not yet been depleted. In other words, the structural affordances of the environment seem to influence the construction not only of search strategies but also of information linked to where the reward is. This observation fits with findings obtained in a different paradigm indicating that efficient explorative behaviors linked to the configuration of the environment are used to build the internal representation of the environment (Mandolesi et al., 2003).

### *Ecology and Search Patterns*

Studies in the area of behavioral ecology have often underlined the need to regard search features as a function of the species' diet and of food resource distribution (Ydenberg, 1998). By considering this eco-ethological approach, rats would perform better in diffuse search spaces, as they are accustomed to forage in wide spaces and in habitats with relatively small food resources (grains, roots, bulbs, insects, larvae) occurring in widely separated clusters. However, it must be taken into account that their foraging behavior is also strongly constrained by the threat of predators. In fact, to escape from predators rats move rapidly and avoid staying in the same location for a long period. This strategy could determine the search behavior observed in the cluster configuration, where the rats tended to abandon a cluster they had not yet completely exploited before moving to the next one. Therefore, food distribution and predatory pressure probably compel rats to compromise between food source exploitation and predator avoidance, splitting their abilities between these opposite demands. An investigation of the "predation hypothesis" by using a predator in a foraging task would be a timely issue for future research aimed specifically at analyzing this ecological threat.

In comparison, monkeys' search efficiency is best expressed in search space organized in clusters (De Lillo et al., 1998; De Lillo et al., 1997). This finding seems to be linked to their frugivorous habits and thus to the need to exploit chunkily distributed resources (De Lillo et al., 1997; Milton, 1993). In contrast, the searching performances of mice are facilitated by regular distribution of food resources (such as that exemplified by a matrix), although with a clustered distribution of food they frequently split search bouts among different clusters (Valsecchi et al., 2000).

### References

- Biegler, R. (2000). Possible uses of path integration in animal navigation. *Animal Learning and Behaviour*, 28, 257–277.
- Brown, M. F., & Terrinoni, M. (1996). Control of choice by the spatial configuration of goals. *Journal of Experimental Psychology: Animal Behavior Processes*, 22, 438–446.
- Brown, M. F., & Winterstein, J. (2004). Spatial patterns and memory for locations. *Learning and Behavior*, 32, 391–400.
- Brown, M. F., Zeiler, C., & John, A. (2001). Spatial pattern learning in rats:

- Control by an iterative pattern. *Journal of Experimental Psychology: Animal Behavior Processes*, 27, 407–416.
- Buzsaki, G. (2005). Theta rhythm of navigation: Link between path integration and landmark navigation, episodic and semantic memory. *Hippocampus*, 15, 827–840.
- Cohen, J., Pardy, S., Solway, H., & Graham, H. (2003). Chunking versus foraging search patterns by rats in the hierarchically baited radial maze. *Animal Cognition*, 6, 93–104.
- Dallal, N. L., & Meck, W. H. (1990). Hierarchical structures: Chunking by food type facilitates spatial memory. *Journal of Experimental Psychology: Animal Behavior Processes*, 16, 69–84.
- De Lillo, C. (1996). The serial organization of behavior by non-human primates: An evaluation of experimental paradigms. *Behavioral Brain Research*, 81, 1–17.
- De Lillo, C., Aversano, M., Tuci, E., & Visalberghi, E. (1998). Spatial constraints and regulatory functions in monkeys' (*Cebus apella*) search. *Journal of Comparative Psychology*, 112, 353–362.
- De Lillo, C., & McGonigle, B. O. (1997). The logic of searches in young children (*Homo sapiens*) and tufted capuchin monkeys (*Cebus apella*). *International Journal of Comparative Psychology*, 10, 1–24.
- De Lillo, C., Visalberghi, E., & Aversano, M. (1997). The organization of exhaustive searches in a patchy space by capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 111, 82–90.
- Denenberg, V. H. (1969). Open field behaviour in the rat: What does it mean? In E. Tobach (Ed.), *Experimental approach to the study of emotional behavior* (pp. 163–174). New York: Ankho International.
- Di Gello, E., Brown, M. F., & Affuso, J. (2002). Negative information: Both presence and absence of spatial pattern elements guide rats' spatial choices. *Psychonomic Bulletin and Review*, 9, 706–713.
- Etienne, A. S., Maurer, R., & Séguinot, V. (1996). Path integration in mammals and its interaction with visual landmarks. *Journal of Experimental Biology*, 199, 201–209.
- European Community Council Directives of November 24, 1986, 609 EEC (1986).
- Greene, C. M., & Cook, R. G. (1997). Landmark geometry and identity controls spatial navigation in rats. *Animal Learning and Behavior*, 25, 312–323.
- Hoffman, C. M., Timberlake, W., Leffel, J., & Gont, R. (1999). How is radial arm maze behavior related to locomotor search tactics? *Animal Learning and Behavior*, 27, 426–444.
- Lachman, S. J. (1965). Behavior in a multiple-choice elimination problem involving five paths. *Journal of Psychology*, 61, 193–202.
- Macuda, T., & Roberts, W. A. (1995). Further evidence for hierarchical chunking in rat spatial memory. *Journal of Experimental Psychology: Animal Behavior Processes*, 21, 20–32.
- Mandolesi, L., Leggio, M. G., Graziano, A., Neri, P., & Petrosini, L. (2001). Cerebellar contribution to spatial event processing: Involvement in procedural and working memory components. *European Journal of Neuroscience*, 14, 2011–2022.
- Mandolesi, L., Leggio, M. G., Spirito, F., & Petrosini, L. (2003). Cerebellar contribution to spatial event processing: Do spatial procedures contribute to formation of spatial declarative knowledge? *European Journal of Neuroscience*, 18, 2618–2626.
- Milton, K. (1993). Diet and primate evolution. *Scientific American*, 269, 70–77.
- Morris, R. G. M., Garrud, P., Rawlins, J. N. P., & O'Keefe, J. (1982, June 24). Place navigation impaired in rats with hippocampal lesions. *Nature*, 297, 681–683.
- Olton, D. S. (1979). Mazes, maps, and memory. *American Psychologist*, 34, 583–596.
- Olton, D. S., & Samuelson, R. J. (1976). Remembrance of places passed: Spatial memory in rats. *Journal of Experimental Psychology: Animal Behavior Processes*, 2, 97–116.
- Parron, C., & Save, E. (2004). Evidence for entorhinal and parietal cortices involvement in path integration in the rat. *Experimental Brain Research*, 159, 349–359.
- Paz-Villagran, V., Save, E., & Poucet, B. (2006). Spatial discrimination of visually similar environments by hippocampal place cells in the presence of remote recalibrating landmarks. *European Journal of Neuroscience*, 23, 187–195.
- Petrosini, L., Molinari, M., & Dell'Anna, M. E. (1996). Cerebellar contribution to spatial event processing: Morris water maze and T-maze. *European Journal of Neuroscience*, 9, 1882–1896.
- Phelps, M. T., & Roberts, W. A. (1989). Central-place foraging by *Rattus norvegicus* on a radial maze. *Journal of Comparative Psychology*, 103, 326–338.
- Roberts, W. A. (1979). Spatial memory in the rat in a hierarchical maze. *Learning and Motivation*, 10, 117–140.
- Roberts, W. A. (1984). Some issues in animal spatial memory. In H. Rotblat, T. Bever, & H. Terrace (Eds.), *Animal cognition* (pp. 425–444). Hillsdale, NJ: Erlbaum.
- Roberts, W. A., & Ilerish, T. J. (1989). Foraging on the radial maze: The role of travel time, food accessibility, and the predictability of food location. *Journal of Experimental Psychology: Animal Behavior Processes*, 15, 274–285.
- Roche, J. P., & Timberlake, W. (1998). Orientation and efficiency: The influence of paths and landmarks on the foraging of Norway rats (*Rattus norvegicus*). *Animal Learning and Behavior*, 26, 76–84.
- Schenk, F., Contant, B., & Grobety, M. C. (1990). Angle and directionality affect rat's organization of visits, sequences and spatial learning in modular mazes. *Learning and Motivation*, 21, 164–189.
- Terrace, H. S., & McGonigle, B. O. (1994). Memory and representation of serial order by children, monkeys, and pigeons. *Current Directions in Psychological Science*, 3, 180–189.
- Timberlake, W., & Hoffman, C. M. (2002). How does the ecological foraging behavior of desert kangaroo rats (*Dipodomys deserti*) relate to their behavior on radial mazes? *Animal Learning and Behavior*, 30, 342–354.
- Timberlake, W., Leffel, J., & Hoffman, C. M. (1999). Stimulus control and function of arm following by rats on a radial-arm floor maze. *Animal Learning and Behavior*, 27, 445–460.
- Timberlake, W., & White, W. (1990). Winning isn't everything: Rats need only food deprivation not food reward to traverse a radial arm maze efficiently. *Learning and Motivation*, 21, 153–163.
- Valsecchi, P., Bartolomucci, A., Aversano, M., & Visalberghi, E. (2000). Learning to cope with two different food distributions: The performance of house mice (*Mus musculus*). *Journal of Comparative Psychology*, 114, 272–280.
- Ydenberg, R. C. (1998). Behavioral decision about foraging and predator avoidance. In R. Dukas (Ed.), *Cognitive ecology* (pp. 343–378). Chicago: University of Chicago Press.

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