

Some factors affecting performance of rats in the traveling salesman problem

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Abstract The traveling salesman problem (TSP) is used to measure the efficiency of spatial route selection. Among researchers in cognitive psychology and neuroscience, it has been utilized to examine the mechanisms of decision making, planning, and spatial navigation. While both human and non-human animals produce good solutions to the TSP, the solution strategies engaged by non-human species are not well understood. We conducted two experiments on the TSP using Long–Evans laboratory rats as subjects. The first experiment examined the role of arena walls in route selection. Rats tend to display thigmotaxis in testing conditions comparable to the TSP, which could produce results similar to a convex hull type strategy suggested for humans. The second experiment examined the role of turn angle between targets along the optimal route, to determine whether rats exhibit a preferential turning bias. Our results indicated that both thigmotaxis and preferential turn angles do affect performance in the TSP, but neither is sufficient as a predictor of route choice in this task.

Keywords Navigation · Cognition · Spatial · Optimization · Strategy · Planning

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Introduction

The traveling salesman problem (TSP) is a complex navigational task that can be used to study spatial cognition and planning. Although the TSP has traditionally been studied by mathematicians and computer scientists, it has more recently drawn the attention of researchers in the fields of cognitive psychology and neuroscience, since it may be useful for examining the mechanisms of various behaviors including learning, decision making, planning, and spatial navigation (MacGregor and Chu 2011; MacGregor and Ormerod 1996). While the bulk of this research has been done with humans, it has also been used in comparative research with rats, pigeons, non-human primates, and other species (e.g., Baron et al. 2014; Gibson et al. 2007; Cramer and Gallistel 1997; Blaser and Ginchansky 2012; Bures et al. 1992; Lihoreau et al. 2012). The goal of the current study was to further examine the strategies used by rats in a TSP task.

The TSP has been proposed as a useful tool for the study of spatial cognition and planning in non-human animals (e.g., Blaser and Ginchansky 2012; Cramer and Gallistel 1997; Gibson et al. 2007; Baron et al. 2014; Miyata et al. 2006). In this task, subjects are required to visit each of several targets arranged in a spatial arena, either virtually on a computer screen or physically in an open field. Depending on task parameters, producing an efficient solution may require learning (about the task requirements), working memory (which targets have already been visited), decision making (which of several options to visit), and planning (which sequence of targets will be visited next). The target configurations, and other parameters such as memory requirements, can be manipulated in order to examine specific strategies that subjects may be using to select routes.

Several strategies have been proposed as mechanisms by which humans or other animals may solve the TSP. These can be broadly categorized as global strategies, in which the subject processes the entire target array at once, and local strategies, in which the subject only takes into account limited information about one or a few targets relative to the subject's current location. It has been argued that humans utilize a global *convex hull* heuristic (MacGregor and Ormerod 1996; MacGregor et al. 2004; Ormerod and Chronicle 1999), which involves linking consecutive nodes along the convex hull (or outer perimeter) of the configuration, and minimizing forays to internal nodes. However, it has also been suggested that humans' apparently global solutions can be accounted for by a simpler tendency to avoid crossing paths (Lee and Vickers 2000; Van Rooij et al. 2003). Most of the research with human subjects suggests that their performance is superior to that produced by very simple local solutions such as the linear nearest-neighbor (NN) strategy, in which the subject always selects the nearest unvisited target (MacGregor and Ormerod 1996). Several hybrid global-to-local strategies have recently been proposed as well, in which subjects move between larger regions using global information and then use a local strategy to navigate within a cluster or region (Wiener et al. 2007; Kong and Schunn 2007).

Compared to humans, non-human animals are less likely to produce near-optimal solutions, but they do distance minimize to some degree, consistently outperforming chance. The performance of pigeons has been reported to be consistent with the use of a NN strategy (Gibson et al. 2007, 2012; Baron et al. 2014; Miyata and Fujita 2010), and some evidence suggests that pigeons can plan ahead at least one subsequent step (e.g., an $N + 1$ strategy). Pigeons also appear to avoid path crossing (Baron et al. 2014) and may therefore use a combination of crossing avoidance and NN (or $N + 1$). Similarly, rats produce solutions that are sometimes consistent with use of the NN, but occasionally superior to it (Blaser and Ginchansky 2012; Bures et al. 1992; de Jong et al. 2011). Another local strategy that has been suggested in rats is a turn-angle preference. This was originally proposed as a bias toward spatial alternation between targets (Bures et al. 1992), but could also involve an 'inertia' strategy, or tendency to keep moving in the same direction when possible (de Jong et al. 2011). Additionally, it has been suggested that rats' tendency to travel along the edges of a standard open field (thigmotaxis) may result in circling the perimeter of the arena, visiting targets along the edges of the configuration in a roughly circular pattern (Blaser and Ginchansky 2012; Ennaceur et al. 2006; Timberlake et al. 1999). This could result in routes similar in form to those produced by humans using a convex hull or crossing-avoidance strategy.

Finally, cluster-based or regional strategies have been proposed for a variety of non-human animals in which the subject attempts to visit the largest number of targets, or gain the largest amount of reward, as quickly as possible (Cramer and Gallistel 1997; Wiener et al. 2004; de Jong et al. 2011). Of course, some combination of these strategies is also possible, such as 'visit the nearest target that is within a certain angle range.'

The purpose of the current experiments was to determine whether two relatively simple local mechanisms, (1) a tendency toward thigmotaxis and (2) a preference for a particular turn angle following reward, could account for rats' better-than-chance performance in the TSP.

Experiment 1

Experiment 1 was designed to examine the role of edge-following in rats' TSP performance. Two square open-field arenas were used: one of which was a traditional walled enclosure to encourage thigmotaxis (walled condition), and the other of which was an elevated arena with no walls to discourage thigmotaxis (open condition). In each arena, the same three target configurations were tested. All configurations included ten targets, with four internal nodes and six along the convex hull. The configurations differed in the number of consecutive convex hull nodes in the optimal solution. In Configuration 1, only two pairs of consecutive convex hull nodes lay along the optimal route. In Configuration 2, two sets of three consecutive convex hull nodes lay along the optimal route. In Configuration 3, five consecutive convex hull nodes lay along the optimal route. See Fig. 1 for an illustration of the three configurations. If thigmotaxis can account for previous reports of good performance in the TSP by producing a 'convex hull-like' route, we predicted generally better performance in the walled condition than in the open condition. Moreover, we predicted we would see the best performance in Configuration 3, where the optimal route was consistent with several consecutive hull-hull transitions. We predicted we would see the worst performance in Configuration 1, where the optimal route required frequent visits to internal targets.

Methods

Subjects

Subjects were 20 male Long-Evans laboratory rats, pair-housed in the University of San Diego vivarium under a 12/12-h light/dark cycle. Subjects were food-restricted to maintain 85 % of ad lib weight, with full water availability throughout the duration of the experiment. Subjects were fed following testing each day. The Institutional Animal

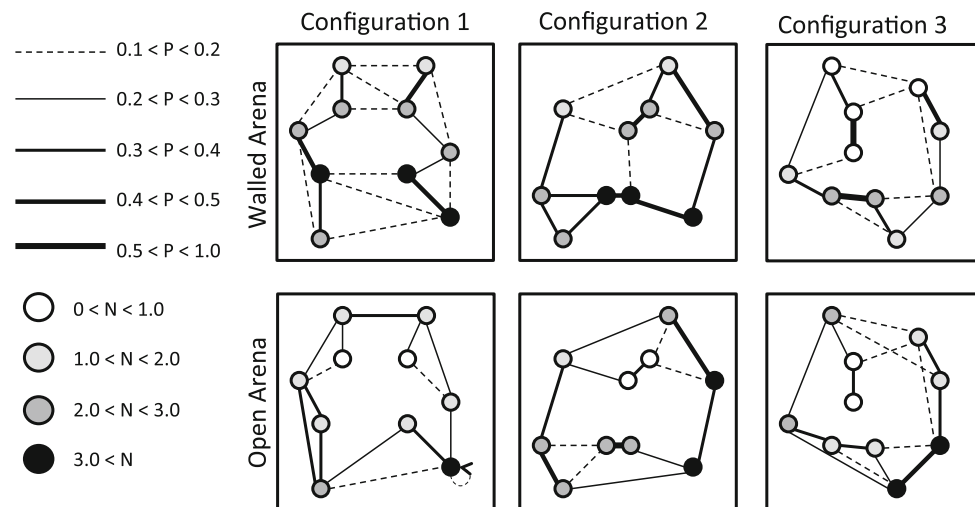


Fig. 1 Configurations 1–3 are illustrated with *lines* between nodes representing the actual transition probabilities between each target pair. The *line weight* connecting each pair of targets represents the transition probability between those two targets, with P ranging from 0 (no transitions between target X and target Y) to 1.0 (all transitions from X are to Y). *Target shading* represents the mean number of visits

to that target, with N of 1.0 representing one visit on average, and $N > 1.0$ indicating revisits. A *line circling* back to the same target indicates the probability of returning directly to that target before visiting any other; this occurred only for the target nearest the start point in the open condition

Care and Use Committee (IACUC) at the University of San Diego approved all experimental protocols.

Apparatus

Experimental apparatus included a $1\text{ m} \times 1\text{ m}$ unwallied open arena elevated approximately 1 m from the floor, and a $1\text{ m} \times 1\text{ m} \times 75\text{ cm}$ ($l \times w \times h$) arena with opaque walls, which was not elevated. Three target configurations were used in Experiment 1 (see Fig. 1). Sterilized bottle caps were used as targets, and pieces of Froot Loops® cereal placed in each target were used as bait. All testing sessions were digitally recorded via camcorder.

Procedure

Habituation and pre-training

Habituation and pre-training occurred over a span of 12 days. Habituation (days 1 and 2) involved placing individual subjects in the walled testing arena for 10 min on Day 1, and the open arena for 10 min on Day 2. Subjects were allowed to freely roam the arena for the entirety of each 10-min session. Habituation was followed by pre-training (days 3–12). On Day 3, subjects were placed in the walled arena with two baited targets and observed for 10 min or until they had removed the bait from both targets (whichever occurred first). Animals that successfully retrieved bait from both targets on Day 3 were then given four baited targets in the unwallied arena on Day 4. Those

that did not retrieve both pieces of bait within the 10-min limit were trained again with two targets on Day 4. In this way, repeating each level until all bait was successfully retrieved, the number of targets was gradually increased to ten. The open and walled arenas were used on alternating days in order to provide exposure to both. In order to complete pre-training and move on to testing, animals were required to successfully retrieve at least 9 of 10 pieces of bait within the 10-min session for 3 days in a row, which all subjects had achieved by Day 12. The spatial arrangement of targets during pre-training was random; therefore, animals received a different arrangement each day, and these were all different from the testing configurations.

Experimental testing

Behavioral testing took place over 6 days, with each subject tested once per day. Every subject was tested twice with each of the three test configurations, once in the walled arena and once in the open arena. The sequence of arena type and configuration was counterbalanced across subjects using a Latin square, so half of the animals encountered a configuration for the first time in the walled arena and half in the open arena. As with pre-training, subjects were individually placed in the testing arena with the targets arranged in the appropriate configuration (illustrated in Fig. 1). All subjects were placed initially into the corner of the arena corresponding with the lower right corner in Fig. 1. Trials concluded after all bait was retrieved, or after a maximum of 10 min. All experimental

sessions were video-recorded and subsequently coded for route selection using the definitions listed below. Throughout pre-training and the tests, the experimenter was stationed in the same room approximately 1 m away from the arena. A random subset of 10 % of video files were coded independently by a second coder in order to establish reliability, which was >90 %.

Definitions of behaviors

A more detailed explanation of route choice calculations, with examples, is provided in Blaser and Ginchansky (2012). The same behavioral measures were used here.

Video coding

Thigmotaxis was defined as the duration of time entirely (all four paws and nose) within the outer 20 cm (approximately body length) perimeter of the arena. *Contact* with a target was recorded when the whiskers, nose, or forepaw of the subject touched either the bottle-cap target or Froot loop[®] bait. Contact with a target by the tail or hind paws of the animal was not counted. *Retrieval* of bait was recorded when the subject removed the bait from the target (so all retrieval scores are automatically counted as contact with that target). Although most of the time (approximately 90 %) the animal paused next to the target to consume the bait, occasionally the subject would carry the bait for some distance before dropping it or consuming it.

Transitions

Transitions were calculated from the sequence of target contacts. A transition was defined as the line segment connecting two consecutive contacts. For example, if a subject contacted Target 2 and then Target 4, a transition from 2 to 4 was recorded. *Optimal Transitions* were the segments connecting target pairs along the optimal route. The distance between each target pair (cm) was used to calculate *total travel distance* for each subject. Because transitions were used to calculate distance measures, these measures did not take into account deviations from the shortest path between two targets.

Memory measures

Revisits were defined as any contact with a target after the bait from that target was retrieved. *Omissions* were defined as any target that was not visited in the 10-min trial period. *Span* was defined as the number of targets visited prior to the first revisit.

Route choice measures

Percent above optimal (PAO) was calculated as the difference between total travel distance and the optimal route distance, divided by the optimal route distance. A lower score indicates better performance, since lower scores indicate shorter path lengths. *Proportion of Optimal Transitions* was calculated as the number of transitions that fell along the optimal route, divided by the total number of transitions. *Proportion of Distance on Optimal* was defined as the total distance travelled along the optimal route, divided by the total travel distance.

Additionally, the frequency of some specific transitions, selected to further examine the roles of the walls, was measured.

H–H The frequency of transitions between two consecutive convex hull nodes. These were subdivided into H–H transitions lying along the optimal route and those that were not on the optimal route. The frequency counts were corrected for the number of possible optimal and non-optimal H–H transitions in each configuration so that scores could be compared. *I–I* The frequency of transitions between two consecutive internal nodes. These were subdivided into I–I transitions lying along the optimal route and those that were not on the optimal route. The frequency counts were corrected for the number of possible optimal and non-optimal I–I transitions in each configuration so that scores could be compared. See Supplementary Fig. 1 for an illustration of H–H and I–I transitions.

Statistics

Thigmotaxis, revisits, omissions, span, PAO, and proportion of optimal transitions were analyzed using a 3×2 (Configuration \times Walls) analysis of variance (ANOVA). Specific transition frequencies (e.g., H–H) were analyzed using a $2 \times 3 \times 2$ (Optimal \times Configuration \times Walls) ANOVA. Distance on optimal was analyzed using a Chi-squared test comparing the actual distribution of transitions in each group with those predicted by chance. The alpha used in the Chi-squared test was 0.008 in order to correct for multiple comparisons. Finally, the correlation between frequency of transitions and the distance of each transition was computed, to determine whether target proximity significantly influenced route choice. Correlations between thigmotaxis and other performance measures (revisits, omissions, PAO, and proportion of optimal transitions) were also computed, to determine whether thigmotaxis was significantly related to individual performance.

Table 1 Experiment 1 results summary

	Walled arena			Open arena		
	Configuration 1	Configuration 2	Configuration 3	Configuration 1	Configuration 2	Configuration 3
Revisits	14.3	20.7	19.6	27.9	29.9	13.2
Omissions	0.4	0.3	0.5	0.2	0.0	0.1
Span	4.8	4.2	4.0	4.8	4.2	4.8
PAO	2.9	3.8	3.9	4.8	4.4	2.3
Proportion optimal	0.48	0.62	0.51	0.55	0.63	0.55
Proportion of distance on optimal	0.34 (0.12)	0.52 (0.13)	0.36 (0.12)	0.37 (0.12)	0.52 (0.13)	0.37 (0.12)
	−0.63	−0.41	−0.40	−0.73	−0.63	−0.60

Results

A summary of the results for Experiment 1 is presented in Table 1.

Thigmotaxis

ANOVA yielded a significant main effect of Walls [$F(1, 17) = 38.30, P < 0.001, \eta_p^2 = 0.68$], with a significantly greater duration near the edges in the walled than the open arena. There was also a significant main effect of Configuration [$F(2, 34) = 24.56, P < 0.001, \eta_p^2 = 0.57$], with the greatest duration near the edges in Configuration 1 and the least in Configuration 3. There were no significant interactions.

Revisits

ANOVA yielded a significant main effect of Walls [$F(1, 17) = 12.57, P = 0.002, \eta_p^2 = 0.42$], with more revisits in the open than the walled arena. There was also a significant main effect of Configuration [$F(2, 34) = 5.21, P = 0.011, \eta_p^2 = 0.23$], with the most revisits in Configuration 2 and the fewest in Configuration 3. There was also a significant Walls \times Configuration interaction, [$F(2, 34) = 6.53, P = 0.004, \eta_p^2 = 0.28$]. The interaction was due to fewer revisits in the walled condition for Configurations 1 and 2 and more revisits in the walled condition for Configuration 3.

Omissions

ANOVA yielded a significant main effect of Walls, [$F(1, 17) = 5.00, P = 0.039, \eta_p^2 = 0.23$], with more omissions in the walled than the open arena. There was no main effect of Configuration and no interaction.

Span

ANOVA yielded no significant effect of either Walls or Configuration on span.

Percent above optimal (PAO)

ANOVA yielded no significant main effects of Walls or of Configuration on PAO, but there was a significant Walls \times Configuration interaction, [$F(2, 34) = 6.34, P = 0.005, \eta_p^2 = 0.27$]. As was the case with revisits, the PAO measure indicates better performance in the walled arena for Configurations 1 and 2, with better performance in the open arena for Configuration 3. These results are illustrated in Fig. 2a.

Proportion of optimal transitions

ANOVA yielded a significant main effect of Walls, [$F(1, 17) = 9.49, P = 0.007, \eta_p^2 = 0.36$], with a significantly higher proportion of optimal transitions in the open condition. There was also a significant main effect of Configuration [$F(2, 34) = 8.29, P = 0.001, \eta_p^2 = 0.33$], with the highest proportion of optimal transitions in Configuration 2 and the lowest in Configuration 3. There was also a significant Walls \times Configuration interaction, [$F(2, 34) = 3.66, P = 0.036, \eta_p^2 = 0.18$]. The interaction was due to a higher frequency of optimal transitions in the open condition for Configuration 1, slightly more frequent optimal transitions in the open condition for Configuration 2, and no difference between conditions for Configuration 3. These results are illustrated in Fig. 2b.

Proportion of distance on optimal

For Configuration 1, 37 % of travel distance in the open arena and 34 % in the walled arena were along the optimal

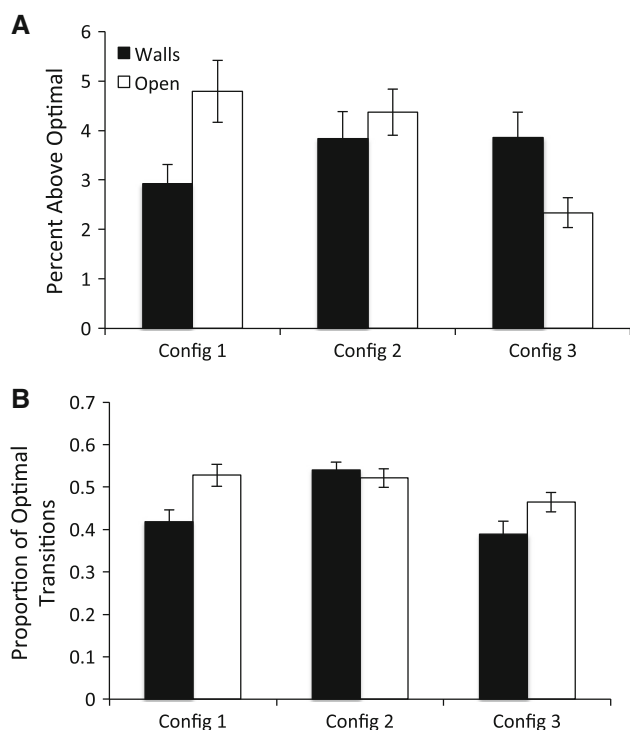


Fig. 2 Performance in Experiment 1 is plotted in this figure. In **a** are the mean percent above optimal (PAO) scores in the walled and open conditions. In **b** are the proportion of optimal transitions in the walled and open conditions. Percent above optimal is lowest (best) in Configuration 1 for the walled condition and in Configuration 3 for the open condition. The proportion of optimal transitions is higher overall in the open condition than the walled condition

route. Both of these differed significantly from the 12 % predicted by chance. For Configuration 2, 52 % of travel distance in the open arena and 52 % in the walled arena were along the optimal route. Both of these differed significantly from the 13 % predicted by chance. For Configuration 3, 38 % of travel distance in the open arena and 36 % in the walled arena were along the optimal route. Both of these differed significantly from the 12 % predicted by chance.

H–H transitions

ANOVA yielded a significant effect of Optimality [$F(1, 19) = 26.12$, $P < 0.001$, $\eta_p^2 = 0.58$], with significantly more optimal than non-optimal H–H transitions. There was a significant main effect of Configuration [$F(2, 38) = 5.26$, $P = 0.010$, $\eta_p^2 = 0.22$], with the most H–H transitions in Configuration 2 and the fewest in Configuration 1. There was a significant main effect of Walls [$F(1, 19) = 27.35$, $P < 0.001$, $\eta_p^2 = 0.59$], with more H–H transitions in the walled arena. There was a significant Optimality \times Configuration interaction [$F(2, 38) = 14.70$, $P < 0.001$, $\eta_p^2 = 0.44$], with virtually no differences between

configurations on the number of non-optimal H–H transitions, but significant variation in optimal H–H transitions across configurations (most in Configuration 2, fewest in Configuration 1). The Optimality \times Walls, Configuration \times Walls, and Optimality \times Configuration \times Walls interactions were not significant. The frequency of H–H transitions is illustrated in Fig. 3a.

I–I transitions

Configuration 1 was excluded from analysis, because there were no optimal I–I transitions. The non-optimal I–I transitions in Configuration 1 were compared across walled conditions by t test, which yielded a significant difference between the walled and the open conditions [$t(19) = 2.91$, $P = 0.009$], with more I–I transitions in the open condition. For Configurations 2 and 3, ANOVA yielded a significant effect of Optimality [$F(1, 19) = 144.77$, $P < 0.001$, $\eta_p^2 = 0.88$], with more optimal than non-optimal I–I transitions. There was also a significant main effect of Configuration [$F(1, 19) = 36.25$, $P < 0.001$, $\eta_p^2 = 0.66$], with more I–I transitions in Configuration 2 than in Configuration 3. There was also a main effect of Walls [$F(1, 19) = 26.49$, $P < 0.001$, $\eta_p^2 = 0.58$], with more I–I transitions in the open arena. There was an Optimality \times Configuration interaction [$F(1, 19) = 26.22$, $P < 0.001$, $\eta_p^2 = 0.58$], with no difference between configurations on non-optimal I–I transitions, but more Optimal I–I transitions in Configuration 2 than Configuration 3. There was a significant Optimality \times Walls interaction [$F(1, 19) = 23.24$, $P < 0.001$, $\eta_p^2 = 0.55$], with no difference between arenas on non-optimal I–I transitions, but significantly more optimal I–I transitions in the open arena. There was a significant Walls \times Configuration interaction [$F(1, 19) = 9.64$, $P = 0.006$, $\eta_p^2 = 0.34$], with the most I–I transitions in the open arena for Configuration 2. Finally, there was a significant Optimality \times Walls \times Configuration interaction [$F(1, 19) = 4.67$, $P = 0.044$, $\eta_p^2 = 0.19$], with the most I–I transitions in the optimal route of the open arena in Configuration 2. The frequency of I–I transitions is illustrated in Fig. 3b.

Correlations

In all six conditions, the frequency of a transition was significantly negatively correlated with its distance, $P < 0.001$. That is, the shorter the distance between two nodes, the greater the frequency of moving between those two nodes. Although thigmotaxis was occasionally significantly related to other performance measures, these correlations were sporadic and, in all cases, negative; that is, more thigmotaxis predicted poorer performance on the task. See Table 2 for the correlation values.

Fig. 3 Mean frequency of specific transitions in Experiment 1 is plotted in this figure. In **a** are hull–hull (H–H) transitions in all three configurations, with optimal H–H transitions on the *left* and non-optimal H–H transitions on the *right*. In **b** are internal–internal (I–I) transitions in all three configurations, with optimal I–I transitions on the *left* and non-optimal I–I transitions on the *right*. The transition frequencies presented here are corrected for the number of optimal and non-optimal H–H and I–I transitions in each configuration by dividing the actual transition frequency by the number of possible transitions in each configuration (Configuration 1 did not include any optimal I–I transitions and is therefore blank)

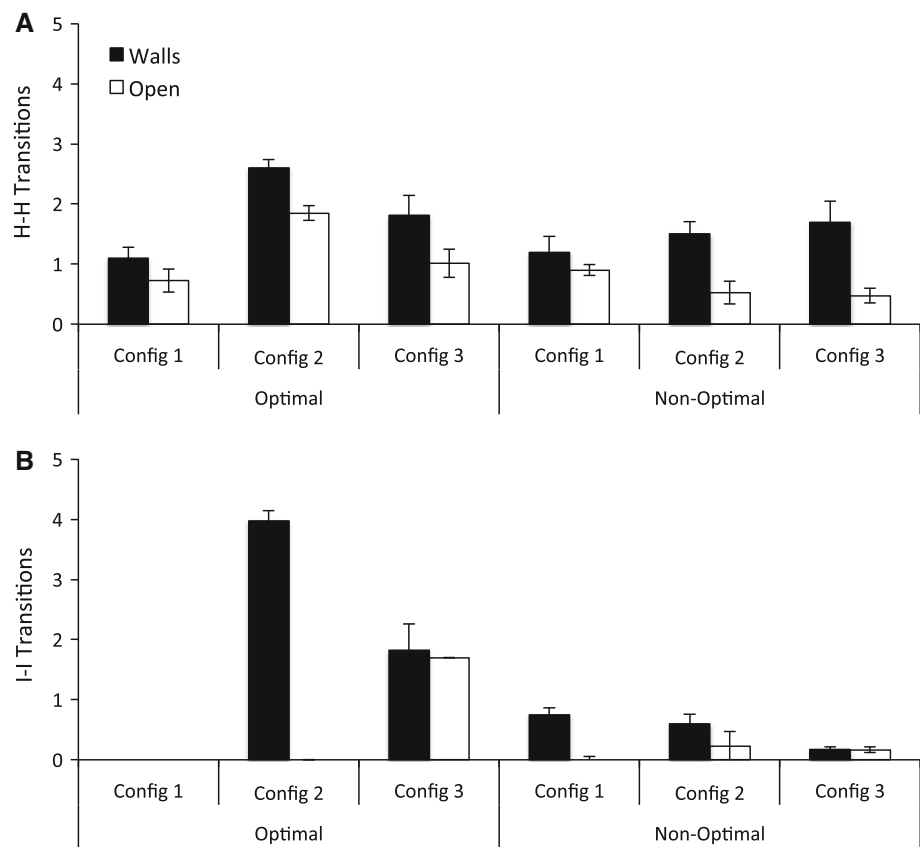


Table 2 Pearson's correlation of thigmotaxis with other measures

	Walled arena			Open arena		
	Configuration 1	Configuration 2	Configuration 3	Configuration 1	Configuration 2	Configuration 3
Revisits	0.13	0.36	0.25	−0.12	0.16	−0.11
Omissions	0.32	0.22	0.11	0.38*	0.31	0.39*
PAO	0.21	0.42*	0.24	−0.10	0.25	0.03
Optimal transitions	0.07	−0.15	−0.01	−0.17	−0.28	−0.48*

* Denotes a statistically significant correlation

Experiment 1 discussion

The results of Experiment 1 make it clear that thigmotaxis is not sufficient to explain rats' performance in the TSP. As expected, rats spent significantly more time near the edges in the walled arena than the open arena, but performance on the TSP was not significantly better in the walled arena. The presence of arena walls did significantly affect several performance measures including revisits, omissions, and route choice, but the effects were mixed, with some improvements and some decrements. Thigmotaxis varied significantly across configurations, with the lowest levels in Configuration 3 and the highest

in Configuration 1, but this did not mirror performance scores; there were fewer optimal transitions in Configuration 3 than in the other two configurations. Finally, while individuals' thigmotaxis scores were not frequently correlated with other performance measures, the few significant correlations were negative—that is, thigmotaxis predicted poor performance. Taken together, it is clear that thigmotaxis occurs in the traditional walled arena and that this can affect route choice in this task, and this should be considered when designing future experiments. However, there is no support for the hypothesis that thigmotaxis can account for subjects' good performance in the TSP.

Experiment 2

Experiment 2 was designed to examine the role of preferential turn angle in rats' TSP performance. Two basic configuration templates were used, each with three variations to produce a total of six testing arrays. In the 'shallow' variation of each configuration, all of the targets were placed along the convex hull, minimizing the turn angle between targets along the optimal route. In the 'middle' variation, five alternating targets were shifted interior to the configuration, producing a moderate turn angle between sequential targets. In the 'sharp' variation, the alternating targets were shifted further interior, producing a sharp turn angle between targets. See Fig. 4 for an illustration of the configurations. If a preferred turn angle can account for performance in the TSP, we expected to see superior

performance in the variation most closely matching the subjects' bias.

Methods

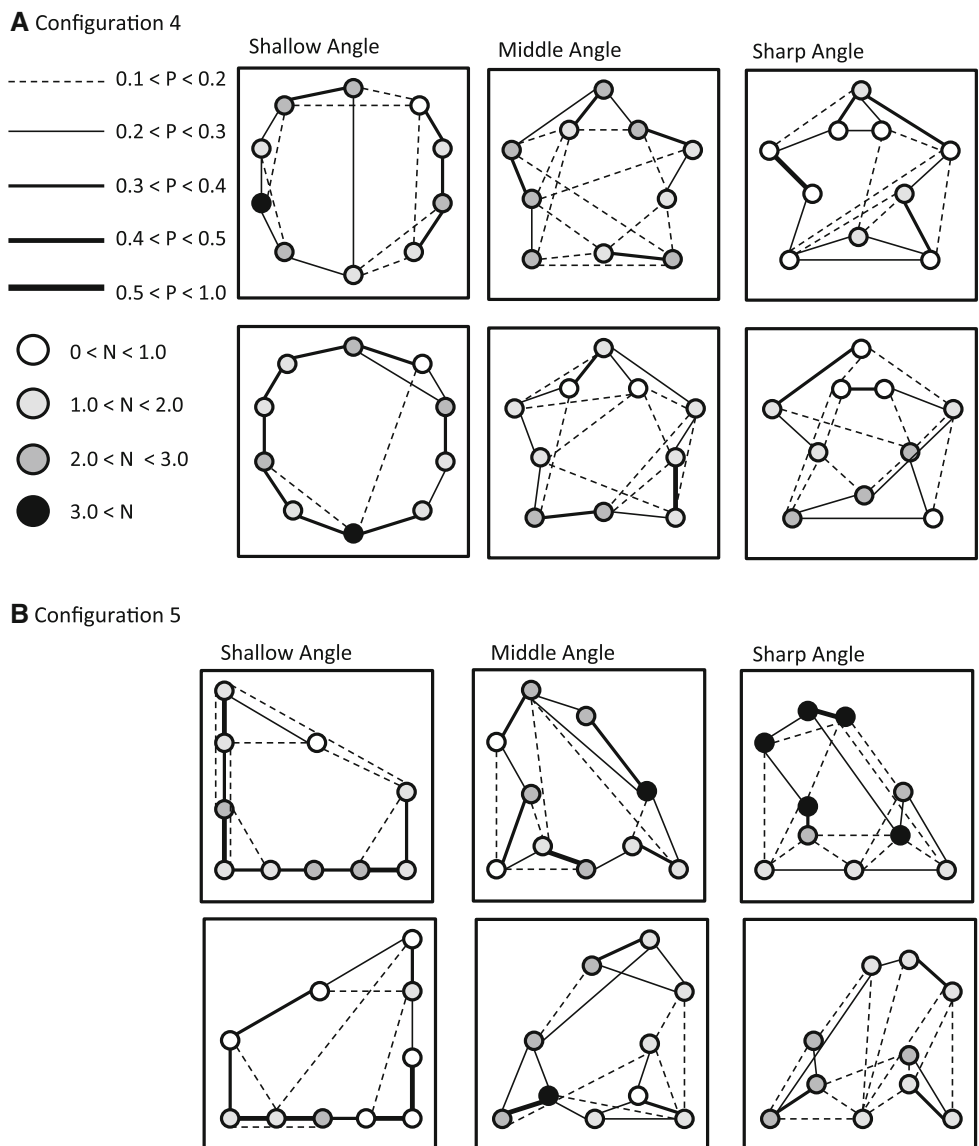
Subjects

Subjects were 16 naive, male Long–Evans laboratory rats living under the same conditions as those in Experiment 1.

Apparatus

The 1 m × 1 m open field was identical to the walled arena used in Experiment 1. Two configuration templates were used in Experiment 2 (see Fig. 4): one symmetrical

Fig. 4 Configurations 4 and 5 are illustrated with lines between nodes representing the actual transition probabilities between each target pair. The original and mirror-image variations of Configuration 4 are represented in (a), while the original and mirror-image variations of Configuration 5 are represented in (b). The line weight connecting each pair of targets represents the transition probability between those two targets, and the target shading represents the mean number of visits to that target



and one asymmetrical. For Configuration 4, the ‘shallow’ variant had a mean turn angle of 143° along the optimal route, the ‘middle’ variant a mean angle of 118° along the optimal route, and the ‘sharp’ variant a mean angle of 89° along the optimal route. For Configuration 5, the ‘shallow’ variant had a mean turn angle of 143° along the optimal route, the ‘middle’ variant a mean angle of 111° along the optimal route, and the ‘sharp’ variant a mean angle of 103° along the optimal route. Each target array was presented to half of the animals in its original form and to the other half as its mirror-image (‘Chirality’) to test for any general right- or left-turn biases. As in Experiment 1, bottle caps and Froot Loops[®] were used as stimuli and all sessions were video-recorded.

Procedure

Habituation and pre-training

Habituation and pre-training proceeded as described for Experiment 1 with the exception that only the walled arena was used. All subjects in Experiment 2 attained training criterion by Day 10 of pre-training.

Experimental testing

Testing occurred over a period of 6 days. Every subject was tested with each of the six test configurations, with configuration sequence counterbalanced across subjects using a Latin square. As in Experiment 1, subjects were placed individually in the corner of the test arena (lower right in Fig. 4) and allowed to forage until all bait was retrieved, or until 10 min had elapsed. Similarly, the researcher remained in the room while behavioral testing occurred. All experimental sessions were video-recorded and subsequently coded for route selection. Once again, a random subset of 10 % of video files were coded independently by a second coder in order to establish reliability, which was $>90\%$.

Definitions of behaviors

Video coding, transition, memory, and route choice measures were all defined as in Experiment 1. A few additional specific transitions were selected to specifically examine the role of turn angle in the results of Experiment 2.

Specific transitions

H–I–H: The frequency of transitions between three consecutive nodes in a (concave) hull–internal–hull angle. *I–H–I*: The frequency of transitions between three consecutive nodes in a (convex) internal–hull–internal angle. *H–I–*

I: The frequency of transitions from the hull to two internal nodes, forming a straight ‘shortcut’ through the configuration (no such transitions were along the optimal route). *H–H–H*: The frequency of transitions between three consecutive hull nodes (no such transitions were along the optimal route). See Supplementary Fig. 2 for an illustration of the transitions that were compared.

Statistics

Revisits, omissions, span, PAO, and proportion of optimal transitions were analyzed using a $3 \times 2 \times 2$ (Angle \times Configuration \times Chirality) analysis of variance (ANOVA). Specific transition frequencies (e.g., I–H–I) were analyzed using a $3 \times 2 \times 2$ (Angle \times Configuration \times Chirality) ANOVA. Distance on optimal was analyzed using a Chi-squared test comparing the actual distribution of transitions in each group with those predicted by chance. The alpha used in the Chi-squared test was 0.008 in order to correct for multiple comparisons. Finally, the correlation between the frequency of transitions and the distance of each transition was computed, to determine whether target proximity significantly influenced route choice.

Results

A summary of the results for Experiment 2 is presented in Table 3.

Memory

There were no significant effects of any variable (Angle, Configuration, or Chirality) on any measures of memory, including revisits, omissions, and span.

Percent above optimal (PAO)

ANOVA yielded no significant main effect of Angle, Configuration, or Chirality on PAO, but there was a significant Angle \times Configuration interaction [$F(2, 14) = 8.88, P = 0.003, \eta_p^2 = 0.56$]. This interaction was due to an improvement in performance as the angle of Configuration 4 decreased (grew sharper), and a decrement of performance as the angle of Configuration 5 decreased. These results are plotted in Fig. 5a.

Proportion of optimal transitions

ANOVA yielded a significant main effect of Angle on the proportion of optimal transitions [$F(2, 14) = 4.46, P = 0.032, \eta_p^2 = 0.39$], with the most optimal transitions in

Table 3 Experiment 2 results summary

	Configuration 4			Configuration 5		
	Shallow	Middle	Sharp	Shallow	Middle	Sharp
Revisits	3.9	4.0	1.8	3.0	4.1	5.1
Omissions	0	0	0	0	0	0
Span	6.8	6.0	8.1	6.9	6.6	7.0
PAO	1.1	0.8	0.5	0.5	0.6	1.0
Proportion optimal	0.62	0.54	0.43	0.71	0.56	0.43
Proportion of distance on optimal	0.39 (0.09)	0.38 (0.12)	0.31 (0.12)	0.52 (0.10)	0.45 (0.14)	0.30 (0.14)
Correlation of transition frequency with distance	-0.72	-0.70	-0.56	-0.70	-0.5	-0.52

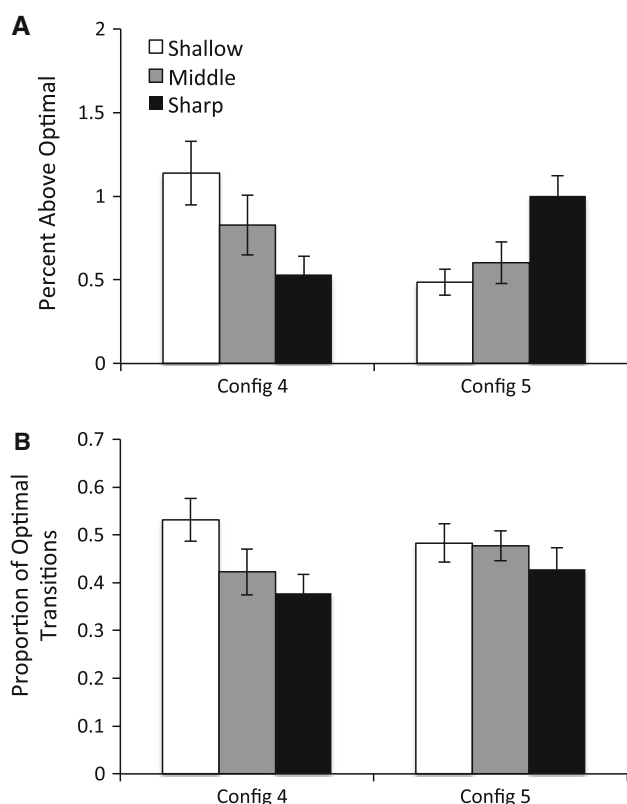


Fig. 5 Performance in Experiment 2 is plotted in this figure. In **a** are the mean percent above optimal (PAO) scores in configurations 4 and 5. In **b** are the proportion of optimal transitions in Configurations 4 and 5. Percent above optimal is lowest (best) in the sharp angle variant of Configuration 4, but best in the shallow angle variant of Configuration 5. The proportion of optimal transitions is higher overall shallow angle variants and lowest in the sharp angle variants

the shallow conditions and the fewest optimal transitions in the sharp conditions. There was no significant main effect of Configuration or Chirality, nor were there any significant interactions. These results are illustrated in Fig. 5b.

Proportion of distance on optimal

For Configuration 4, 38 % of travel distance was along the optimal route in the widest angle condition, 32 % in the middle angle condition, and 24 % in the sharpest angle condition. These all differed significantly from the 9 % predicted by chance. For Configuration 5, 50 % of travel distance was along the optimal route in the widest angle condition, 34 % in the middle angle condition, and 23 % in the sharpest angle condition. These all differed significantly from the 9 % predicted by chance.

H–I–H transitions

There was no main effect of Configuration, but there was a main effect of Angle [$F(2, 14) = 12.56$, $P < 0.001$, $\eta_p^2 = 0.64$], with fewer H–I–H transitions as the sharpness of the angles increased. There were no other main effects or interactions. The frequency of H–I–H transitions is illustrated in Fig. 6a.

I–H–I transitions

There was no main effect of Configuration, but there was a main effect of Angle [$F(2, 14) = 10.42$, $P = 0.002$, $\eta_p^2 = 0.60$], with fewer I–H–I transitions as the sharpness of the angles increased. There were no other main effects or interactions. The frequency of I–H–I transitions is illustrated in Fig. 6b.

H–I–I transitions

There were no significant effects on H–I–I transitions.

H–H–H Transitions

There were no significant effects on H–H–H Transitions.

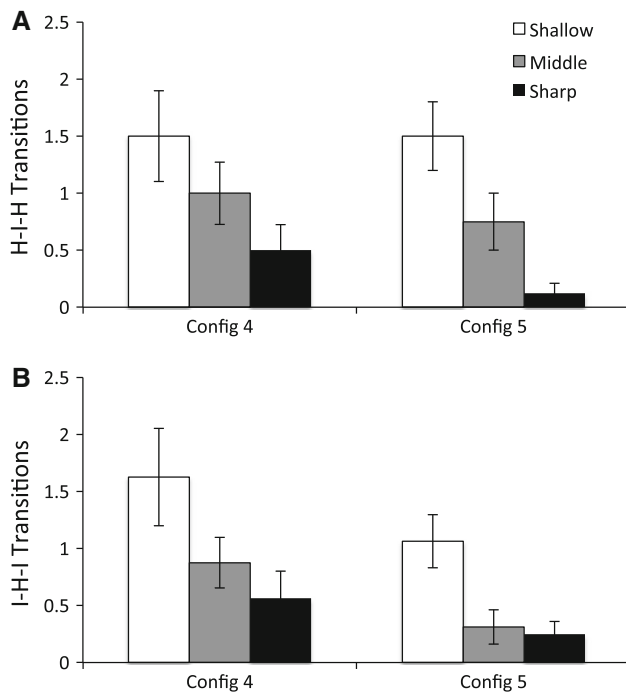


Fig. 6 Mean frequency of specific transitions in Experiment 2 is plotted in Fig. 6. In **a** are hull–internal–hull (H–I–H) transitions and in **b** are internal–hull–internal (I–H–I) transitions. There are an equal number of H–I–H and I–H–I transitions across configuration variants, so no corrections of the scores are used

Correlations

In all six conditions, the frequency of a transition was significantly negatively correlated with its distance, <0.001 . That is, the shorter the distance between two nodes, the greater the frequency of moving between those two nodes. See Table 2 for the correlation values.

Experiment 2 discussion

As with thigmotaxis in Experiment 1, it is clear that a turn-angle bias is insufficient to explain route choice in the TSP. Neither distance nor memory measures varied significantly with turn angle. Animals demonstrated some preference for shallow angles, selecting more optimal transitions in the shallow than sharp turn conditions. However, this preference did not lead to a significant tendency to select non-optimal shallow angles. Additionally, the interaction effect of angle and configuration on PAO scores indicates that the spatial array of targets modulated the role of turn angle. The overall pattern of results indicates that while turn angle does affect route choice, with a preference for straighter paths, some additional strategy is involved.

General discussion

Experiment 1 was designed to determine whether thigmotaxis is a dominant strategy used by rats for route selection in the TSP. Because following the convex hull can generally result in distance minimization in the TSP, it is possible that the simple bias toward edge-seeking could account for the better-than-chance performance observed in rats, without requiring a true distance-minimization strategy or planning (Blaser and Ginchansky 2012; de Jong et al. 2011; Bures et al. 1992). If performance of rats in this task can be attributed to thigmotaxis, (1) performance scores should mirror thigmotaxis scores across conditions, with better performance in the walled arena, (2) there should be more total transitions between consecutive hull nodes in the walled condition, independently of whether these transitions lie along the optimal route, and (3) performance on Configuration 3 in the walled condition should be best, since its optimal route included the most consecutive hull transitions.

While our results do suggest that thigmotaxis affected route choice in this task, it is clear that the subjects did not use this as the primary basis for target selection. Although animals did remain significantly nearer the edges in the walled arena, task performance measures were not consistently affected by the presence of walls. Memory measures were mixed, with significantly more revisits, but significantly fewer omissions, in the open arena than the walled arena (see Table 1). Other measures of memory and distance showed no overall effect of walls on performance. Finally, individual thigmotaxis scores were not correlated with better performance in any of the experimental conditions.

Subjects did select transitions between consecutive hull nodes (H–H transitions) significantly more often in the walled condition than the open condition; similarly, they selected transitions between consecutive internal nodes (I–I transitions) significantly more often in the open condition (see Fig. 3). These results provide evidence that the presence of walls affected their route choice to some degree. However, this effect was dependent on whether the transitions were on the optimal route; animals in both walled and open conditions still selected optimal H–H and I–I transitions significantly more often than non-optimal transitions. Therefore, while thigmotaxis played a role in route selection, animals were clearly sensitive to additional factors that led to distance minimization. Taken together, the results of Experiment 1 clearly demonstrate that rats use a distance-minimization strategy in the TSP that goes beyond a simple thigmotaxis tendency. The simplest explanation may be the use of an NN or $N + 1$ strategy that competes with thigmotaxis-induced circling (de Jong et al. 2011; Bures et al. 1992), to produce a hybrid strategy.

Experiment 2 was designed to determine whether turn-angle preference could be a dominant strategy used by rats to distance minimize in the TSP task. If rats have a preference for changing their direction of movement following each reward, this could lead to enhanced performance on configurations whose optimal routes follow a path that alternates between hull and internal nodes. In this case, rats should select more H–I–H and I–H–I transitions when these form sharp angles (direction changes) than when they form a relatively straight line. Conversely, if rats have a preference to continue moving in a straight line when possible, they should show better performance on configurations whose optimal routes involve relatively shallow turns, and they should select more H–I–H and I–H–I transitions when these form shallow angles.

As in Experiment 1, the results indicate that target selection is influenced by turn angle to some degree, but do not support this as a dominant strategy for route selection. There were no main effects of Angle on any measures of memory or distance. Angle did affect the tendency to select optimal H–I–H and I–H–I transitions, with these transitions selected more frequently when the angles were shallow than when they were sharp. Therefore, the general tendency was to prefer moving in a relatively straight line than to change directions between targets. However, there were virtually no differences between conditions on non-optimal transitions—so despite their preference for straight angles, subjects were still sensitive to whether those trajectories were consistent with distance minimization. Therefore, a preference toward straight angles, such as the preference for thigmotaxis, is still subordinate to some additional distance-minimizing strategy (Gallistel and Cramer 1996), which is in accord with previous research indicating that distance minimization is a key factor in route selection by rats (de Jong et al. 2011; Bures et al. 1992).

In sum, our results indicate that rats are using a route selection strategy that cannot be explained by the mechanisms of thigmotaxis or a preferred angular movement alone. Although previous studies have also indicted that rats do not solely rely on a NN heuristic to navigate in the TSP (Blaser and Ginchansky 2012; de Jong et al. 2011), it is possible that the animals are using a hybrid strategy in which the distance to the nearest target(s), turn angle to those targets, and proximity to the arena border, all contribute to target choice. Of course, additional strategies, such as including global processing or planning beyond the NN level (i.e., $N + 1$ or $N + 2$), should also be considered for future research.

Compliance with Ethical Standards

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in

accordance with the ethical standards of the institution or practice at which the studies were conducted.

Conflict of interest The authors declare that they have no conflict of interest.

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