Brief report

The sectored foraging field: A novel design to quantify spatial strategies, learning, memory, and emotion

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Abstract

Although Norway rats are naturally gregarious, males typically live alone at some point during adulthood. Different social ecologies often require different learning strategies and also modulate response to stressors and gonadal development. To measure effects of the social environment on the interaction between cognition and emotion during aging, we focused on a natural learning context and devised the sectored foraging field, a progressively difficult spatial navigation task. Here, we describe how this apparatus and protocol permits multiple learning strategies in a minimally stressful environment, enabling finely graded analyses of cognition and emotionality. Male Sprague–Dawley rats living alone throughout adulthood adopted a sex-typic discernible spatial strategy. In contrast, males housed in group contexts utilized an algorithmic kinesthetic strategy, repeating the same motor action until they found food. Removal of food and distal, but not local cues, elicited anxious alertness, particularly in group-housed males. Cognitive performance of group-housed rats subsequent to food and cue removal was significantly impaired, yet enhanced in isolates.
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Norway rats (*Rattus norvegicus*) thrive in a variety of social contexts (Barnett, 1963; Steineger, 1950; Telle, 1972). Some live as social isolates, particularly during the mating season, others live in groups (Barnett, 1963; Calhoun, 1962). As it is well established that social ecology affects foraging strategies (Coraco & Wolf, 1975), we hypothesized that living alone or in groups throughout adulthood would produce individual variation in spatial strategies and emotional reactions to cognitive challenges. Sustained housing of male laboratory rats in group cages lacks the environmental complexity needed to support many species-typic social and dominance interactions (Hediger, 1964; Ziporyn & McClintock, 1991). In addition, this psychosocial context increases aggressive interactions accompanied by surges in corticosterone levels and dominance related changes in gonadal weight (Stefanski, 2000; Wood, Young, Reagan, & McEwen, 2003). The hippocampus, a structure which subserves spatial strategy, is sensitive to corticosterone from physical and psychosocial stressors (Isgor, Kabbaj, Akil, & Watson, 2004; Touyarot, Venero, & Sandi, 2004) as well as androgens (Kerr, Allore, Beck, & Handa, 1995; Leranth, Petnehazy, & MacLusky, 2003; Nagdhi, Nafisy, & Majlessi, 2001).

Unfortunately, using a highly stressful and aversive task, such as the Morris water maze to test animals with different social histories and hormonal levels could mask their effects on spatial strategy (Kavaliers, Perrot-Sinal, & Ossenkopp, 1996). In addition, traditional runway mazes do not facilitate behaviors indicating the rat's emotional state during the cognitive challenge. Our goal, therefore, was to design a task that minimized

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performance stress while remaining sufficiently sensitive to detect individual differences in spatial strategies and emotional responses to risk.

The sectored foraging field (SFF) retains key features of prior successful tests of spatial cognition. These features are: unconstrained movement (e.g., Morris water maze and Barnes maze), discrete choices (e.g., Olton radial arm maze and plus maze), and movable local and distal cues. Reducing aversive motivation (drowning, food deprivation, and escape) is critical for avoiding masking effects of stress on cognitive function and detecting individual differences in emotional reactions to a new environment (Cavigelli & McClintock, 2004). Consequently, rats were motivated to forage for a highly preferred food treat, but were not food-deprived nor required to escape from the maze. There was a large open area in the center, as would be found in a foraging environment, that presented an aversive risk in this thigmotactic species.

To assess cognitive load, difficulty was increased in four phases. Rats first explored the large open field using a variety of strategies to find eight-baited sites. Second, the addition of barriers transformed it into an analogue of the radial arm maze, while retaining an open field in the center large enough to make some strategies more aversive than others (i.e., crossing the open field vs. hugging the walls and sampling serially each compartment). Third, we reduced the number of baited locations from eight to one. Fourth, we removed distal and local cues as well as the food.

Specifically, a circular piece of coated wood (4 ft. diameter), mounted on casters, formed the field's platform. Eight baited food cups around the outer edge could be separated by 12″ removable clear acrylic, "L-shaped" dividers (Fig. 1A). The platform could be turned independently from its surrounding 18″ high clear acrylic wall. Removable local cues in various shapes, sizes, textures, and colors were attached near the wall (Fig. 1A). Distal cues were furniture and patterns mounted on the walls of the large rectangular room (Fig. 1B) and hidden by a black curtain suspended from a circular frame attached to the ceiling.

The reward (part of a Fruit Loop) was placed in a bait cup. Each had a plastic grid, covering additional Fruit Loops, precluding odors as positional cues (Kirwan, Gilbert, & Kesner, 2005). We also eliminated rat odor trails as memory cues by mixing the bedding before each trial and baiting the same location in the room, not the same cup, by rotating the castor-mounted platform to a random position. The entire testing apparatus was cleaned daily and before trials without local or distal cues. The animal was carried from a resting station to the center of the testing apparatus, facing a randomly assigned sector.

Cognitive load increased as rats progressed through training and testing, affording quantification of learning
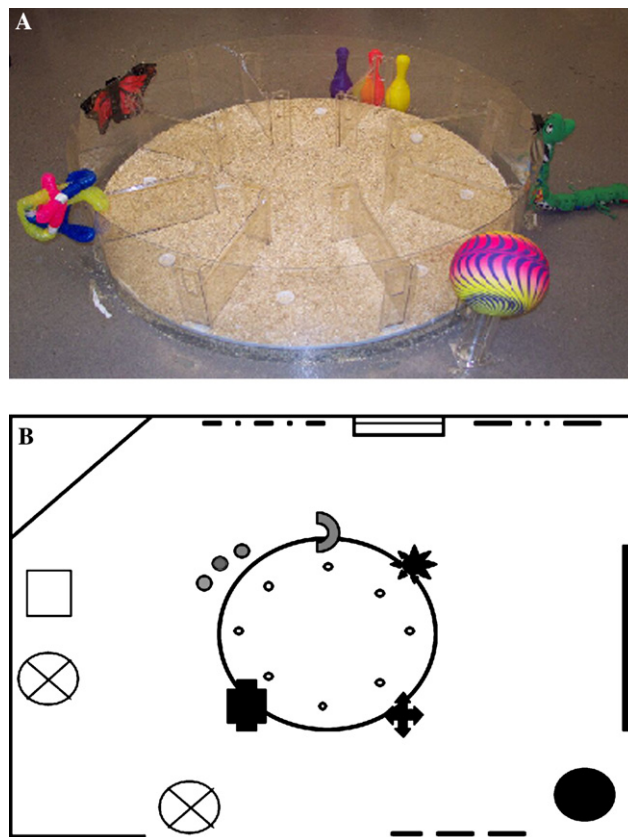

Fig. 1. (A) Sectored Foraging Field with its dividers, open field at center, and a variety of removable local landmark cues. Distal cues are arrayed along the walls of the room. (B) Schematic diagram of the relationship between the foraging field and the geometry of the testing room.

rates, and development of cognitive strategies in a progressively complex environment. The phases also tapped different memory systems: spatial working memory was assayed in the eight-location phase (as in an Olton radial arm maze) while the one-location phase required reference (as in the Morris water maze). Training and testing proceeded as follows:

Habituation to novel food treat: Reward verification: One cereal piece was hand fed to each rat daily for one week in its home cage, to familiarize it with the food treat. All readily ate the treat, with no detectable differences.

Training phase 1: Food location: All cup locations were baited without sector dividers and rats foraged for treats (Trial 1 lasted until all eight baited locations were found; subsequent trials were limited to 3.5 min). Promotion criterion to Barrier Phase was locating all eight bait cups within 2 min (63% of all rats) or exceeding 20 total trial minutes (37% of all rats).

Training phase 2: Barrier phase: Dividers between sectors were added, keeping the food locations the same. Training was continued, limiting trials to 3.5 min. Promotion criterion to Specific Location Phase was locating

all eight bait cups within 3.5 min (80% of all rats) or exceeding 30 total trial minutes (20% of all rats).

Testing: Specific location phase: Each animal was randomly assigned a single food location relative to the room and then trained to criteria locating the single food source. Promotion criterion to the Cue Dependence and Food Removal Test was consistently locating food within 30 s (25–45 trials) (90% of all rats) or exceeding 45 total trial minutes (10% of all rats). (Phase 1 through the testing phase represents the learning portion of the task.)

Probe: Cue dependence and food removal test: The test comprised 20 trials in four sets of five. The first and third sets were uninterrupted, and each trial ended as soon as the rat located the food or 3 min had elapsed. In the second and fourth sets, no food cup was baited and either local or distal positional cues were removed in a single 3-min trial, during the 2nd, 3rd, or 4th trial of the session. The order of removing local or distal positional cues was counterbalanced across animals, as was trial number during which they were removed.

A grid system quantified the animal's foraging path from sector to sector. In general, animals used one or more of three clearly identifiable foraging strategies during a given trial: (1) Bisecting: The rat bisected the open field moving in a straight line from one sector to another creating paths of intersecting triangles and skipping a minimum of two adjacent sectors (Fig. 2A); (2) Sequential Sampling: The rat sequentially sampled each location in every sector or every other sector through a series of clockwise or counter-clockwise turns. More efficient animals often backed out of quadrants in the absence of a food cache (Fig. 2A); (3) Freezing: The rat froze in position and did not forage. A well-established ethogram of sniffing, rearing, grooming, and freezing quantified attentional and emotional states. The following experiment exemplifies data obtainable with the Sectored Foraging Field. Data from the memory and a Cue Dependence Test are presented here; detailed results from all phases are outside the scope of a Brief Report on the apparatus and protocol.

Male Sprague–Dawley rats lived in their assigned social conditions from 1 to 17 months of age; 10 in 2 non-crowded groups (cage $46 \times 61 \times 36$ cm), 10 isolates in standard single cages ($26 \times 23 \times 22$ cm). Food and water were available ad libitum. All lived in the same laboratory room 23 °C, 50% relative humidity; 14:10 h light:dark cycle (lights on 1000 h CST). All training and testing was done in the dark phase (behavioral "day" in this nocturnal species). Seventeen males completed testing; at necropsy isolated males had smaller testes than animals in groups (2.67 ± 0.18 g vs. 3.37 ± 0.08 g, $t = 3.7$, $p = .003$).

When cues and food were present, isolated males were four times more likely to bisect the open field to locate the food bait than group-housed males ($60.6 \pm 12.3\%$ of trials by isolated males; $13.2 \pm 8.3\%$ of trials by grouped-
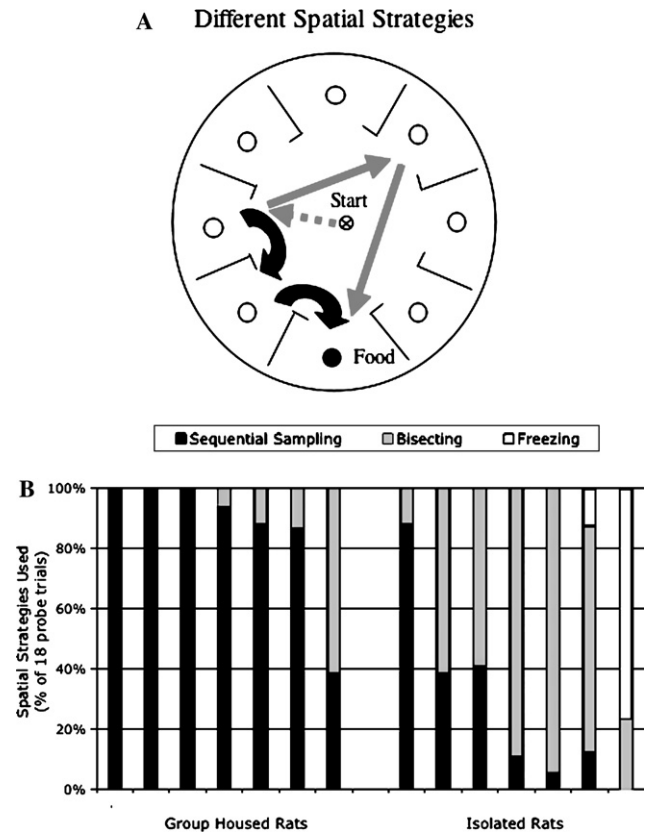

Fig. 2. (A) Animals placed in the center of the open field in a random orientation relative to the compartment with the food. They located the food using either a predominantly bisecting (left) or sequential sampling strategies (right) to localize the baited food cup. The bisecting strategy appears to be Euclidean, allowing a destination to be reached from different starting points using different paths. (B) Summary of foraging strategies used by socially isolated and group housed males.

housed males, $t = 3.20$, $p < .01$, see Figs. 2A and B). In marked contrast, group-housed males adopted a sequential sampling strategy ($86.8 \pm 8.3\%$ of trials by grouped males; $28.5 \pm 11.6\%$ of trials by isolated males, $t = 4.09$, $p < .002$, see Fig. 2B). Nonetheless, isolated and grouped males were equally efficient in locating the food reward (isolated males average latency to locate the food reward 20.63 ± 4.60 s; group-housed males latency 21.12 ± 11.44 s, $t = 0.04$; $p \leqslant .97$).

When the food bait was absent and either local or distal cues were removed, both group-housed and isolated males exhibited behaviors indicating emotional states ranging from anxious attention to fear. Removing food and either type of cue increased the number of cups sniffed, as well as stereotyped grooming indicative of mild anxiety in all males. However, when distal, rather than local, cues were missing, males were more likely to rear up, stand on their hind legs, and survey the environment ($F(1, 23) = 29.2$, $p < .0001$). This was particularly true for group-housed males, who reared more often overall, indicating higher levels of anxious alertness

(main effect of housing $F(1, 23) = 10.0$, $p \leqslant .005$; interaction of housing and type of cue $F(1, 23) = 5.79$, $p \leqslant .03$). This anxious alert behavior did not simply reflect greater motor activity as neither housing nor type of cue removal affected how many sectors were visited (all F's $\leqslant 1.2$, all p's $\geqslant .28$). Moreover, group-housed males did not rear more often than isolates in a previous test of open field behavior (Hermes, 2003).

The removal of food bait and cues had opposite effects on performance efficiency of isolated and grouped males. After distal cues returned, isolated males found the food 50% faster (reduction of 21.2 ± 7.76 s), whereas group-housed males took significantly longer (increasing 30.6 ± 22.3 s; Mann Whitney U test, $U = 3.00$, $p = .01$). Thus, group-housed males took five times longer to locate the food cache than the isolates (45.1 ± 20.7 s vs. 9.2 ± 4.4 s; Breslow–Gehan–Wilcoxon, $\chi^2 = 4.8$, $p \leqslant .05$). Removal of local cues had no effect on subsequent foraging efficiency; isolated males (0.7 ± 6.89 s faster vs. 1.57 ± 11.55 s slower, Mann Whitney U test, $U = 21$, $p = 1.00$).

In sum, both socially isolated and group-housed males were more sensitive to distal than local cues, as reported in previous studies of sex-specific strategies in laboratory rats (Jacobs, 2003). Nonetheless, social condition affected the use of such cues and affective responses to their removal. Isolates reared-up only a moderate amount when distal cues were removed and their performance improved significantly upon their return. They used a sex-typic discernible spatial strategy, using external cues to locate food and bisecting a mildly threatening open field to obtain it. Group-housed males were significantly more anxious, rearing twice as much when distal cues were removed, and their performance declined dramatically upon their return. This is particularly remarkable because they used sequential sampling, an algorithmic kinesthetic strategy in which the same motor action is repeated until the food is found and thought to be independent of distal cues (Thinnus-Blanc, 1996).

In general, studies of hippocampal function have shown that the predominant strategy used by isolates represented a more robust hippocampal response. Intact male rats in the radial arm maze have shown a bisecting or 'spatial' strategy (Jarrard, 1993). The sequential or algorithmic strategy used by group-housed males in this study is one that has been found in mice with hippocampal damage on the radial arm maze (Etchamendy, Desmedt, Cortes-Torrea, Marighetto, & Jaffard, 2003). Another interpretation is that the group-housed males did not differentiate distal from local cues, but encoded them together as a single visual snapshot. When distal cues were removed, these rats thus lost their orientation and were not able to restore it after the cues were replaced. Such pattern completion is hypothesized to be subserved by the CA3 subfield of the hippocampus, a subfield which may also underlie the encoding of distal cues by male rats (Nakazawa et al., 2002). Consistent freezing behavior was detected in a single isolated male in this small sample. The only instance in which this isolated male was ambulatory was in the absence of local and distal cues, suggesting that this individual had a unique response to the task; more data are required to elucidate the neuroendocrine basis of these differences.

The sectored foraging field proved to be a powerful tool for demonstrating that social conditions create marked individual differences in cognitive appraisal and emotional reactions during navigation. It offers a new environment and context for quantifying this interplay of emotion and cognition during learning and memory tasks. Recent publication of the rat genome (Gibbs, Weinstock, Metzker, Muzny, & Sodergren, 2004) makes this species and finely graded analyses of cognition and emotion of considerable value for evaluating the interaction of genetic, neural, and endocrine mechanisms.

Acknowledgments

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