Rats of the Dark Agouti strain were trained on delayed alternation under conditions that should encourage egocentric working memory. In two experiments a T-maze was set within a cross-maze so that different arms could be used for the sample and test runs. The maze had high opaque side-walls, and testing was conducted in low light levels so that distal visual cues might be eliminated. By rotating the maze 90° between the sample and choice run and by using two identical mazes set side by side it was possible to nullify other spatial strategies. Experiments 1 and 2 showed that rats preferentially used place information, intramaze cues, and direction cues, even though only egocentric or idiothetic (nonmatch-to-turn) working memory could successfully solve every trial. Rats were able to maintain an accurate sense of location within the maze even though distal cues were not visible and the animal was moved between the sample and choice runs. Experiment 2 confirmed that another rat strain (Long-Evans) shows the same learning profiles. Both experiments indicate that rats are very poor at using either egocentric or idiothetic information to alternate, and that retention delays as short as 10 s can eliminate the use of these forms of memory.
strategies by which the task could potentially be solved (Dember & Fowler, 1958; Douglas, 1966; Dudchenko & Davidson, 2002; Restle, 1957). These strategies include place alternation, response alternation, local cue (intramaze cues such as odour trials) alternation, and direction alternation (using a set heading direction from which to alternate, e.g., go east then west). The present study sought to examine the balance between these strategies under conditions that should encourage the use of egocentric and idiothetic information.

An egocentric strategy is defined here by whether or not a choice is at a particular angle or vector from the rat’s starting position (in the case of a T-maze, 90° to the left or 90° to the right from the end of the start arm). An idiothetic strategy differs from an egocentric one in that a choice is based on past movement (in the case of a T-maze, body turn to the right or to the left). For T-maze alternation this idiothetic strategy is assumed to be reliant on interoceptive cues generated by the animal turning to the right or left. Thus, idiothetic alternation can be regarded as nonmatch-to-turn while egocentric alternation is nonmatch-to-vector. In the case of T-maze alternation these two strategies cannot readily be distinguished as the start arm ensures that the animal is always positioned at 90° to the choice it has to make, and these choice directions are then limited by the floors of the maze. Furthermore, both strategies should be applicable, even under very low light levels. “Direction” alternation (e.g., go east then west) is a special case of egocentric alternation as it will only be effective if the start run is in the same direction for both the sample and test phases.

Although a nonmatching-to-turn or nonmatching-to-vector strategy will solve alternation tasks, there is a long-standing debate over the extent to which such strategies actually aid rats on tasks such as T-maze alternation (Dember & Fowler, 1958; Douglas, 1966; Dudchenko, 2001; Restle, 1957). The rationale for the present study was prompted by the renewed interest in the neural basis of rodent egocentric working memory and its differences with other forms of spatial memory (e.g., Kesner, Hunt, Williams, & Long, 1996; Ragozzino & Kesner, 2001; Rasmussen, Barnes, & McNaughton, 1989), coupled with the unresolved debate over how readily rats can actually use these forms of memory (Baird, Futter, Muir, & Aggleton, 2004; Dudchenko, 2001). For these reasons the present task deliberately incorporated features likely to discourage the use of place cues while ensuring that egocentric or idiothetic working memory could correctly guide performance throughout testing. The T-maze used throughout the study was composed of three arms from a cross-maze. This made it possible to use four different start arms for the sample and choice trials and so vary systematically how much place, intramaze, and direction cues could aid performance. It is, for example, possible to create trial types in which egocentric and place cues are congruent in supporting alternation, while in others they are set in opposition.

In Experiment 1, Dark Agouti rats were trained to nonmatch-to-turn/nonmatch-to-vector under low light levels. For some trials the maze was rotated between the sample and choice trials, so setting intramaze and place cues in conflict. The final training stages used two identical cross-mazes placed side by side to remove intramaze cues. The primary goal was to determine the balance of strategies used, although only egocentric cues or nonmatching-to-turn would always produce the correct solution. Experiment 2 had two goals that were both in response to the apparent difficulty that rats had in using these strategies in Experiment 1. The first was to limit even further the use of other cues to solve the alternation task in the hope that this would further encourage egocentric or turn alternation. The second goal was to test the generality of the findings from the first experiment, and so in Experiment 2 two rat strains (Long-Evans and Dark Agouti) were compared. The Long-Evans strain was chosen as it has been argued that on some spatial tasks its performance not only closely resembles that of wild-type rats but it is significantly different to that of Dark Agouti rats (Harker & Whishaw, 2002).
EXPERIMENT 1

Each trial consisted of a forced sample run followed by a choice run in which nonmatching to the turn made in the sample run was always rewarded. Training was carried out in a cross-maze in which the entrance to each arm could be blocked, so that four distinct T-mazes could be created. The maze was placed on a turntable so that the maze could be rotated during the retention interval (between the forced and choice runs). Later in training, two adjacent cross-mazes were used so that the sample run was in one maze, and the choice run was in the adjacent maze. In this way all intramaze cues for that trial could be removed. As a further modification all mazes had high side-walls, and testing was conducted in low light levels. These features were to limit the availability of distal cues that might overshadow learning of the idiothetic or egocentric rule. Although all trials could be correctly solved by egocentric nonmatching or nonmatching-to-turn, the contributions from place, intramaze, and directional cues were systematically altered by changing the start arms, rotating the maze, and using two mazes.

Method

Subjects
A total of 6 male rats of the pigmented Dark Agouti strain (Bantin and Kingman, Hull) were used. The rats were naïve at the start of behavioural training. At the start of testing animals weighed approximately 250 g and were approximately 3 months old. Rats were housed in pairs and maintained at their approximate 85% free-feeding weight with water provided ad lib. Home cage lighting was under a 14-hr light/10-hr dark regime.

Apparatus
Two identical cross-mazes were used during the course of Experiment 1. The floors of both mazes were made from wood and were painted white. Each arm was 45.5 cm long and 12 cm wide. The sidewalls were made from black Perspex and were 32.5 cm high. At the end of each arm was a sunken food well, 2 cm in diameter and 0.75 cm deep. Four metal supports raised the floor of the maze 81.5 cm above the ground.

The first part of the experiment used a single cross-maze positioned in the centre of the test room (297 × 293 × 255 cm). In the later part of the experiment the two cross-mazes were placed side by side in the same experimental room (45 cm apart at the closest point). During initial acquisition dim lighting was provided by a shielded standard lamp (60-W bulb) placed on the floor of the test room under the maze. When two mazes were used a lamp was placed under each maze. The luminance in the middle of the cross-maze was 0.85 lux.

Procedure

Habituation. Pretraining began with 2 days habituation to the maze in the light with the food wells in all four arms baited with sucrose reward pellets (45 mg, Noyes Reward Pellets, Lancaster, NH). During each habituation period, which lasted 10 min, the sucrose pellets were continuously replaced so that no arm was found to be empty when first visited.

Acquisition: General methods. Rats were first trained with 8 trials per session (acquisition: Sessions 1–11), but this was then increased to 12 trials for all remaining stages (Sessions 12–72). This increase in trial number was to provide even greater exposure to the task rules. Within the 72 training sessions there were six stages. These stages in chronological order were: acquisition, Probe I, rotation–Probe II, two-maze learning, two-maze 10-s delay, and two-maze retest. Throughout training rats only received one training session per day.

Throughout this experiment a trial consisted of giving the animal a forced “sample” run followed by a “choice” run. Forced turns were made by partitioning off one of the side arms of the cross-maze and the arm that was always opposite to the start arm. The partitions were made of opaque Perspex that slotted into the arms at the junction of the
cross. After turning down the preselected arm the animal was allowed to eat two sucrose pellets that had previously been placed in the food well. Animals were then picked up from the end of the forced-choice arm and returned to a preselected start arm. Animals were then given a free choice between the right and left turn arms, receiving a reward (three pellets) if they turned in the direction opposite to that in the sample run (i.e., nonmatching). For Sessions 1–43 only one maze was used, but for all remaining sessions two mazes, placed side by side, were used. For these sessions (44–72) the sample turn was in one cross-maze while the choice run was in the other.

At the start of each session all 6 rats were taken from the holding room to the experimental room in an enclosed carry-box made of aluminium. The box contained six compartments, and each one had a roof so that the animal could not see out. The carry-box was placed on a table behind the cross-maze during testing. All 6 rats were tested together with each rat having one trial in turn, so that the intertrial interval (ITI) ranged from 2–4 minutes. Each day contained an equal number of forced right or left turns in a pseudorandom sequence.

**Acquisition**

All rats received 11 sessions, each session containing eight trials. The interval between the end of the forced turn and the start of the choice run was typically 3 s. The correct arm for the choice phase was prebaited before both components of the trial. This was possible because in this stage both the forced turn and the choice run for a given trial were started from the same start arm (north or south). These two different arms were used in an intermixed order so that equal numbers of trials (forced turn and choice) were run from either the north or the south arms. The east and west arms were not used as start arms at any stage in training as their usage on the subsequent two-maze condition would lead to longer delays between the sample and choice runs than would occur with the north and south arms. This difference arises from the greater distances required to move the animals on some trials between the sample and choice runs.

**Probe I**

The first probe series was to test whether the rats were relying on egocentric/idiographic cues. For these trials (Sessions 12–23) the forced sample turns were still started from either the north or the south arms, but now the choice run began from any of the four arms. There were thus eight different trial conditions that could be grouped into four different categories of probe trial (see Figure 1). For Probe Types 1 and 2 the correct choice was an arm that had not been used in the forced turn nor had the arm location been used. As a consequence not only egocentric/idiographic but also intramaze or place alternation would result in a correct choice. For Probe 1, but not 2, direction cues would also support performance. The situation for Probes 3 and 4 was very different as for both of these probes intramaze and place alternation would lead to an incorrect choice (see Figure 1). In addition, direction cues do not support Probes 3 and 4, and it has been assumed that moving the animal 90° or 180° negates the value of directional information but need not make performance worse (Dudchenko & Davidson, 2002). For this reason direction effects in Probes 2–4 are labelled as “neutral”. Within each session of 12 trials the rats received an equal number of these four probe types in a pseudorandom sequence. When possible (Probes 1 and 2) the correct, choice arm was prebaited (i.e., before both the forced turn and the choice run), but the arrangement of start arms within a trial precluded this sometimes (Probes 3 and 4).

The first six sessions of Probe I were run with the same room conditions as those used for acquisition. For the last six probe sessions the room lighting was changed by replacing the single white bulb with a 60-W red light. The luminance at the cross point in the maze was now 0.74 lux.

**Probe II (rotation)**

In Probe I, the intramaze and place cues always acted in the same direction. By rotating the maze 90° either clockwise or anticlockwise between the forced sample run and the choice run it was possible to put these cue types into conflict (Sessions 24–43). This rotation procedure was applied to
the four probe types described in Probe I, resulting in eight rotation probe types. These rotation types are depicted in Figure 2, where it can be seen that the correct run directions form four matched pairs (Rotations 1 & 8, 2 & 7, 3 & 6, 4 & 5). Each of these pairs involved the same sample run with the test run from the same position, the difference being whether the maze was rotated 90° clockwise or anticlockwise (see Figure 2). Each session consisted solely of rotation probes, with the different types being given in a counterbalanced, changing sequence. Equal numbers of right and left maze rotations were used within each session. This procedure continued for 20 sessions with rats receiving 12 trials per session. For the last five sessions, and thereafter, the room lighting was reduced further to minimize any possible use of visual cues (luminance in the middle of the cross-maze was 0.65 lux).

From Figure 2 it can be seen that the eight rotation types provide all combinations of when particular cues (direction, intramaze, place) are supporting or are in conflict with the correct choice (always a nonmatch-to-turn). For Rotation Probe 4 all four cue types support the correct choice, for Rotation Probes 1 and 5 three cue types support performance, for Rotations 2, 3, and 8 two cue types support performance, and for Rotations 6 and 7 only egocentric nonmatching will give the correct arm choice.

Two-maze learning
In order to remove intramaze cues that could guide performance, different mazes were used for the forced and choice runs (Sessions 44–60). Rats were initially habituated (Session 44) to a second cross-maze placed in the same room and position as those for the original maze (see Figure 3). For the remainder of this condition (Sessions 45–60) the two cross-mazes were placed adjacent to each other in the same room. The forced-turn phase of a trial was run in one maze, and the choice phase was completed in the other maze. The order in which the mazes were used was counterbalanced, with the forced turn always starting from either the north or the south arm of one maze and the choice run from the other maze. The east and west arms were not used for the start of the sample run as these would result in having to move the animals a greater distance to the other maze and so might interfere with egocentric or idiothetic strategies. The appropriate arms were baited prior to the sample run.

In order to limit the distance that the animal had to be moved during the retention interval not all arm combinations were used between the forced and choice runs. Thus, if the forced run was in Maze 2 then the start arm used for the choice run in Maze 1 would be north, south, or east. Conversely, if the forced run was in Maze 1 the choice run in Maze 2 would start from north, south, or west. This resulted in eight trial types of four basic types (see Figure 3). The way in which place and direction cues might help or
hinder egocentric alternation is shown in Figure 3. For place information it has been assumed that the rats treat the two mazes as if they were a single maze in the same location, although this is not the only possibility. It is again assumed that direction cues either can aid performance if sample and choice are run in the same direction (Probes A, B; Figure 3) or can be regarded as neutral (Probes C, D; Figure 3). The time taken to move the rat from the end of the sample run to the start of the choice run was approximately 3 s.

After six sessions the number of trial types was reduced in order to focus on those most likely to rely solely on egocentric cues (Types C and D,
Figure 3. These 10 additional sessions (51–60) consisted of the forced turn being started from either the north or the south arms of Mazes 1 or 2. The rats were then moved to the adjacent maze and started in either the east or the west arm (depending on the forced-turn maze, see above) for the choice run. Trial Types A and B were not included as rats could potentially use room direction cues as the sample and choice runs started in the same direction (Dudchenko & Davidson, 2002; i.e., alternate east then west rather than right then left).

10-s delay
Using exactly the same procedure as that used for Sessions 51–60 (Trial Types C and D only), the rats received 10 sessions in which a delay of 10 s was now added between the forced turn and the choice run (Sessions 61–70). For the first five sessions the experimenter held the rat for the 10-s retention interval. For this, rats were held firmly and close to the body of the experimenter, to avoid unnecessary movements, before being placed in the start arm for the choice run. This ensured that the rats maintained the correct orientation, although it may have been more stressful. For the last five sessions the rat was placed immediately into the start arm for the choice run. The rat was then held in the start area for 10 s by a barrier preventing the rat from moving down the arm to the choice point. While this variant was assumed to be less stressful, the
animal was free to turn around during the 10-s period.

Retest: No delays
Rats were tested for a final 2 sessions (71–72), using exactly the same procedure as that used for the last 10 sessions of the two-maze condition (Sessions 51–60). Thus the minimum retention interval was returned to 3 s.

Results

Acquisition
The rats’ performance improved with training (one-way analysis of variance, ANOVA; effect of session $F(10, 55) = 4.79, p < .001$, so that the last three sessions exceeded 90% (Figure 4). The daily scores were significantly above chance from Session 3 onwards (66%), $t(5) = 3.73, p = .013$.

Probe I
The sessions for Probe I have been pooled as altering the room illumination (from Session 18) did not affect overall performance, $F(1, 286) = 1.10, p > .1$, or performance on the various probe types ($F < 1$). Consistent with this lack of difference, performance levels remained stable (mean = 57%) across the probe sessions as shown by the lack of an effect of session, $F(11, 276) = 1.03, p > .1$. While overall performance remained significantly above chance $t(5) = 3.46, p < .05$, it was lower than that at the end of acquisition (vs. last six sessions of acquisition phase), $F(1, 115) = 90.1, p < .001$.

There were highly significant differences in performance levels between the four probe types (Figure 5); $F(3, 284) = 41.15, p < .001$. The rats performed Probe Types 1 and 2 significantly above chance: Probe Type 1, 81%, $t(71) = 9.04, p < .001$; Probe Type 2, 70%, $t(71) = 6.02, p < .001$. In both of these probe types, place and intramaze alternation would aid performance. In addition, simple effects showed that Probe 1 performance was significantly higher than Probe 2 ($p < .05$), suggesting that direction cues could also aid performance (Figure 5). In contrast, performance on Probe Types 3 and 4 was significantly below chance: Probe Type 3, 37%, $t(71) = -3.91, p < .001$; Probe Type 4, 38%, $t(71) = -3.03, p < .005$. In both of these trial types the correct choice involved selecting an arm that not only had the animal run down as part of the forced phase but was in a more recently visited location.

Rotation: Probe II
This condition used the same four test types as those in Probe 1 but with one important change: The maze was rotated by 90°, either clockwise or

Figure 4. Initial acquisition of forced alternation showing the mean ($\pm$ SEM) percentage of correct scores across the first 11 sessions. Chance was 50%.

Figure 5. Mean ($\pm$ SEM) percentage of correct responses for all trials from each of the four probe types from Probe I, Experiment 1. Chance was 50%. The histograms include how potential cues could aid (+) or confound (−) the correct response in the choice phase. It is assumed that direction cues either aid (+) or have no effect (N).
anticlockwise after the sample run. This addition makes it possible to separate the effects of place and intramaze cues. Maze rotation produces eight probes, which are in fact matched pairs of the original four probes of Probe I. Within these matched pairs there are, however, differences of cue compatibility. For example, Rotation Probes 1 and 8 are matched with respect to the sample and choice phase, but differ in the availability of intramaze cues. In Rotation Probe 1 the intramaze cues could support the rat when making a correct choice, whereas in Rotation Probe 8 intramaze cues oppose the correct response (assuming that rats avoid recently visited cues). These similarities and differences are mirrored for all four matched pairs (1 with 8, 2 with 7, 3 with 6, and 4 with 5).

The 20 sessions were combined (Figure 6) to form one data set as performance was stable across sessions ($F < 1$). Performance did, however, differ significantly between the eight rotation probe types, $F(7, 131) = 13.05$, $p < .001$. While performance on Rotations 1, 3, 4, 5, and 6 were all significantly above chance (Figure 6), minimum $t(16) = 2.31$, $p < .05$ for Rotation 3, Rotations 2 and 8 did not differ from chance (Figure 6). The poorest performance was on Rotation 7, which was significantly below chance, $t(16) = -2.24$, $p < .05$. The finding that for three conditions performance was not above chance indicates that performance was not controlled by egocentric or idiothetic cues, and so the influence of other factors was considered.

The experimental design created complementary pairs of tests, so it was possible to balance some factors while considering a specified factor on its own. Three factors were considered: (a) whether the correct arm in the choice run was an arm that the rat had already been in as part of the forced-turn run (intramaze cues); (b) whether the correct arm in the choice run was in a location that the rat had already been in as part of the forced-turn run (place cues); (c) the degree of rotation the rat went through when being transferred from the end of the sample run to the start of the choice run.

1. Intramaze cues. The rotation probes could be divided into those in which the animal was rewarded for running into an arm that it had just been in as part of the forced run (Rotations 5, 6, 7, 8) and those in which a new arm was the correct choice (Rotations 1, 2, 3, 4). Performance was significantly higher for those trials in which the correct arm had not already been traversed on the sample run (not previously visited, 66%, previously visited, 58%), $F(1, 137) = 6.25$, $p = .01$.

Within the group with previously visited arms there is a subtle distinction between whether the repeat arm was the arm that the animal started from on the sample run (Rotations 5 and 6) or whether it was the arm that the animal was forced into to find food on the sample run (Rotations 7 and 8; see Figure 2). From Figure 6 it can be seen that performance on Rotations 7 and 8 (select baited arm) was considerably poorer than that on Rotations 5 and 6 (select start arm). Other evidence for this difference comes from the comparisons between Rotations 2 and 7, 1 and 8, 4 and 5, and 3 and 6. For all of these comparisons the principal difference is the presence (5, 6, 7, 8) or absence of intramaze cues (1, 2, 3, 4). When the intramaze cues refer to the
baited arm (2 vs. 7, 1 vs. 8) these differences are significant, $F(1,32) = 7.03, p < .05$, $F(1, 32) = 19.8, p < .001$, respectively. When the intramaze cues refer to the start arm (4 vs. 5, 3 vs. 6) these differences are not significant (both $F < 1$). These comparisons strongly suggest that the rats will use intramaze cues to avoid a previously visited arm, but only if it was the arm in which they were fed.

2. Place cues. By rotating the maze between the sample and choice runs it was possible to create trials in which the rat had to run back into an arm that was in the same physical location as that where it had come from but contained no familiar intramaze cues or vice versa. The eight rotation types can be divided into four groups (see Figure 7) by how the available cues could support alternation: Rotations 1, 4, both intramaze and place cues; Rotations 2, 3, intramaze but not place cues; Rotations 5, 8, place but not intramaze cues; Rotations 6, 7, neither intramaze nor place cues. (For these comparisons direction cues, which might aid Rotation Types 4 and 5, were ignored.) The mean percentage correct scores for these four classes of probe trial are shown in Figure 7. Performance between these four categories differed significantly, $F(3, 44) = 6.44, p < .005$, as the condition where both intramaze and place cues aided performance led to superior performance when compared to those conditions when just intramaze cues or neither set of cues supported alternation (Newman–Keuls test). No other comparisons were significantly different (Figure 7). Although these three other categories (place cues only, intramaze cues only, and neither cue type) did not differ significantly from one another, they were not equivalent as performance was significantly above chance when either place cues ($p = .012$) or intramaze cues ($p = .051$) supported alternation alone (Figure 7). When neither cue type supported performance (Rotations 6, 7), the overall rate of alternation was not above chance.

There was, in addition, evidence that the rats were especially unwilling to return to certain locations. In particular, the rats avoided returning to the arm that was in the same location as that of the initial arm on the sample run (Rotations 2 and 7). This can be seen when Rotation 6 (63%) is compared with 7 (43%), $F(1, 34) = 19.51, p < .001$, and when Rotation 3 (62%) is compared with 2 (53%), $F(1, 34) = 4.47, p < .05$. In both cases the rats are avoiding the arm that was in a location in which the rat was never rewarded throughout acquisition (Sessions 1–11).

3. Degree of animal rotation. Three different degrees of animal rotation occurred between the end of the sample and the start choice runs ($0^\circ$, $90^\circ$, $180^\circ$, Figure 2). For two probes there was no rotation ($0^\circ$) as the rats started from where they finished the choice run (matched pairs: Rotations 2 and 7). In four probe types (matched pair, Rotations 3 and 6; matched pair, Rotations 4 and 5) the rats were rotated through $90^\circ$, while for the two remaining probes (matched pair: Rotations 1 and 8) the rats were moved by $180^\circ$. These different rotation types were then matched in pairs, ensuring that although they differed for degree of rotation, they had comparable contingencies for place and intramaze cues. This produced four comparison pairs: Rotation 2 ($0^\circ$) versus 3 ($90^\circ$); Rotation 7 ($0^\circ$) versus 6 ($90^\circ$); Rotation 4 ($90^\circ$) versus 1 ($180^\circ$); Rotation 5 ($90^\circ$) versus 8 ($180^\circ$). Combining these four
pairs forms two sets (i.e., 0° and 90°, and 90° and 180°). No consistent support was found for the prediction that performance would decline with increased rotation as accuracy was higher on trials where the rat was rotated through 90° than where it was rotated through 0°, $F(1, 68) = 11.35, p = .001$. Performance was also better in those rotation trials with 90° than in those with 180°, $F(1, 68) = 7.35, p < .01$.

Two mazes

The results from both sets of previous probe trials strongly indicate that the rats were sensitive to some intramaze cues. In order to remove these cues the remaining conditions used a change of maze between the sample run and the choice run. This manipulation should leave only egocentric and idiothetic cues (Sessions 45–60) as the only consistent predictors of the correct choice, although place and direction cues could affect individual trial types. In order to predict the effect of place cues it has initially been assumed that rats treat the two mazes as if they were in the same location (i.e., not side by side). From this assumption it can be predicted that the Trial Types A and B will have the highest accuracy and that they should be equivalent (see Figure 3). The next best should be Trial Type D, with Type C the poorest (i.e., $A = B > D > C$, see Figure 3).

Over the first six sessions (45–50) of the two-maze condition training performance remained stable (effect of session, $F < 1$). Overall performance was significantly above chance (mean 62%), $t(5) = 5.45, p < .005$. While trials of Types A and B (see Figure 8) were significantly above chance: A, 71%, $t(35) = 4.86, p < .001$; B, 68%, $t(35) = 3.91, p < .001$, trials of Types C and D did not differ from chance: C, 55%, $t(35) = 1.36, p = .18$; D, 58%, $t(35) = 2.00, p = .053$. This difference was reflected in a significant effect of trial type, $F(3, 105) = 4.61, p = .01$. Performances of trials of Types A and B were significantly higher than those of trials of Types C and D, but there were no other differences. One consistent difference between these two groups of trial types is that only for A and B are the sample and choice runs in the same initial direction (see Figure 3).

When rats were solely trained (Sessions 51–60) on those trial types most likely to demand egocentric behaviours (i.e., trials of Types C and D, Sessions 51–60) overall performance decreased (57.5%). Nevertheless, the scores for both trial types (C and D) were now above chance, D, 59%, $t(59) = 3.41, p < .005$, or closely approaching significance, C, 56%, $t(59) = 1.99, p = .051$.
Delay (10 s) and retest (no delay)

Over the first five sessions (rats held) with a 10-s delay, overall performance did not differ from chance (51.9%), $t(5) = 0.97$, $p > .05$. The same was true for the next five sessions (rat kept in start box) with a 10-s delay as performance again did not exceed chance (53.3%), $t(5) = 1.11$, $p > .05$. There was no difference in the overall performance for the first and second block of five sessions (Figure 8; $F < 1$). Combining all 10 sessions still failed to produce performance above chance (52.6%), $t(5) = 1.17$, $p > .05$.

All rats finally received two sessions (retest), exactly the same as in the delay condition except that the 10-s delay was removed. Now performance was significantly above chance (61%), $t(5) = 2.42$, $p < .05$.

Discussion

Experiment 1 demonstrates that rats are biased by multiple forms of spatial cues when solving a nonmatching-to-turn task in a T-maze, set within a cross-maze. These cues potentially consist of intramaze cues, place cues, direction cues, idiothetic cues, and egocentric cues. Of these, the last two appeared to have the least discernable influence, even though they were the only cue types that could solve every trial. Evidence that alternation performance was dominated by place cues and by intramaze cues came from Probe I and from comparing the rotation probes. Thus, for place cues the animals avoided entering an arm that was in a location (place) that they had occupied during the sample run. This effect was found even though all training was under conditions in which distal visual cues would have been extremely difficult to use. For intramaze cues the rats avoided entering an actual arm that they had already visited on the sample run (intramaze). The rotation probes indicated that the influence of these two cue types was comparable in the present conditions. There was also evidence that the aversion for intramaze cues was strongest when the rat had eaten in that arm.

Even though both egocentric and idiothetic cues could have been used to guide successful performance on every trial, there was little evidence that these forms of information readily support alternation performance. Indeed, when opposed by place and intramaze cues (see Figure 5), performance was sometimes significantly below chance. Nevertheless, evidence for egocentric/idiothetic working memory was obtained from the two-maze condition. This evidence only emerged when intramaze cues were removed (by having two mazes) and when the value of place information was nullified by only using two conditions (C and D) that would have opposing interactions with place information. Even so, this form of information appears to be easily disrupted and only transient, as delays as short as 10 s reduced performances to chance. This result is in close agreement with a previous study (Baird et al., 2004), which also found that nonmatching-to-turn was extremely difficult to learn, only led to low levels of performance, and had a very rapid rate of decay. It should be added that the rapid rate of forgetting in the present study is unlikely to be due to any increase in stress associated with the enforced delay, as a similar rapid loss of performance was found for a nonmatching-to-turn task in which the rats were not handled during the delay (Baird et al., 2004).

An additional influence came from direction cues. This refers to the situation where the sample and choice runs begin in the same direction, even if it is not in the same maze (Douglas, 1966; Dudchenko & Davidson, 2002). The possible involvement of directional cues could be seen in the very first probe after initial acquisition, as Probe Type 1 was superior to Probe Type 2 (Figure 5), one of the key differences being the consistency in direction of the runs for the sample and choice phases. Probably the strongest evidence for the use of direction cues came from the two-maze manipulation, where Conditions A and B (Figure 3) led to superior performance over Condition D. Although Douglas (1966) recommended caution about assuming that directional cues could aid in the forced-choice alternation task, as well as in spontaneous alternation, the present results support the view that this class of cue can be used across both
types of alternation task (Dudchenko & Davidson, 2002). The present data also suggest that turning the rat by 180° does not cause the rat to bias its choices in the opposite direction (i.e., is not more disruptive than a turn of 90°). A similar result was noted by Dudchenko and Davidson (2002).

The rotation probes made it possible to set intramaze cues against place cues. A general prediction that performance is the summation of place, intramaze, and direction cues for alternation finds considerable support in the pattern of results (Figures 5, 6, 7). Within the rotation probes the only clear exception was Probe 6, where performance was higher than expected. For Rotation Probes 6 and 7 both place and intramaze cues opposed the correct choice, yet it was only on Probe 7 that performance was significantly below chance. At present we cannot account for this difference.

One potential shortcoming is that the results may have been specific to the strain of rat. This is a plausible possibility as strain differences have been reported for the performance of allocentric spatial tasks (Harker & Whishaw, 2002). Experiment 2 sought to determine the generality of the present findings by comparing two strains. In addition, the training conditions were slightly modified to discourage further the use of place or intramaze cues.

EXPERIMENT 2

One possible explanation for the apparent inability of the rats in Experiment 1 to engage egocentric or idiothetic strategies readily is that this reflects a unique feature of the Dark Agouti strain. A recent comparison of different rat strains showed sensory and behavioural differences between several inbred and outbred strains (Harker & Whishaw, 2002; Prusky, Harker, Douglas, & Whishaw, 2002). To address the issue of behavioural differences between strains we repeated parts of Experiment 1 but compared two rat strains, Dark Agouti and Long-Evans. The Long-Evans strain was chosen as it has been used for previous egocentric memory studies (Kesner, Farnsworth, & DiMattia, 1989; Kesner et al., 1996; Ragozzino & Kesner, 2001), and, as claimed, it may more closely resemble wild type rats in its profile of spatial performance (Harker & Whishaw, 2002). The two rat strains were also compared on their levels of activity in a novel environment to help establish that these strains do have different phenotypes (Harker & Whishaw, 2002).

Method

Subjects
A total of 8 male rats of the pigmented Dark Agouti (DA) strain (Bantin and Kingman, Hull) and 8 male Long-Evans (LE) rats (Charles Rivers, Margate) were used. The rats were naïve at the start of behavioural training. At the start of testing the rats weighed approximately 250 g (DA) and 375 g (LE) and were approximately 3 months old. Rats were housed in pairs and were maintained at their approximate 85% free-feeding weight with water provided ad lib. Home cage lighting was under a 14-hr light/10-hr dark regime.

Spontaneous locomotor activity
The day before beginning habituation all rats were placed individually in activity boxes set in a novel room for a period of 1 hour. All animals were again tested the day after T-maze testing had finished. Therefore, a measure of spontaneous locomotor activity was taken for both strains pre- and postexperiment.

Egocentric alternation
Apparatus
The cross-maze apparatus was the same as that used for Experiment 1. The first part of the experiment (acquisition) used a single maze positioned in the centre of the test room (297 × 293 × 255 cm). In the latter part of the experiment two cross-mazes were placed side by side in the same experimental room. Dim red lighting was provided by a shielded standard lamp (60-W bulb) placed on the floor of the test
room under the maze throughout the experiment. When two mazes were used a lamp was placed under each maze. The luminance in the middle of the cross-maze was 0.67 lux.

**Procedure**

**Habituation.** Pretraining differed slightly from that in Experiment 1. Pretraining began with 10 days habituation. The first 7 days involved rewarding the rats for running down a straight runway on six successive trials in the dark. This was to encourage the rats to be active in the dark and to not jump out of the apparatus. For the next three sessions rats were placed in the cross-maze for 10 min in the dark, and the food wells in all four arms were baited with sucrose reward pellets (45 mg, Noyes Reward Pellets, Lancaster, NH). During this habituation period the sucrose pellets were continuously replaced so that no arm was found to be empty when first visited.

**Acquisition: General methods.** Rats were first trained with eight trials per session (acquisition: Sessions 1–20); this number of trials was used through all sessions with the exception of Sessions 37–48, when the trial number was increased to 12. This change was to increase the exposure of the rats to the nonmatching rule and so aid learning. All trials were spaced, with about 3 min between trials, to reduce interference effects. Within the 75 training sessions there were six stages. These stages in chronological order were: acquisition, two-maze learning (8 and 12 trials per session), room transfer, 10-s delay, and retest.

Throughout this experiment a “trial” was identical to that of Experiment 1 in that the rat was forced in a predetermined direction for the sample run and then had to turn in the opposite direction in the choice phase of a trial to gain a reward of sucrose pellets. For Sessions 1–20 only one maze was used, but for all remaining sessions two mazes, placed side by side, were used. The forced turn was in one maze while the choice run was in the other maze.

At the start of each session rats were taken in groups of four (two Dark Agouti and two Long-Evans) from the holding room to the experimental room in an enclosed carry-box made of aluminium. The box contained four compartments, and each one had a solid roof so that the animal could not see out. The carry-box was placed on a table behind the cross-maze during testing. Each group, comprising 4 rats, was tested concurrently with each rat having one trial in turn. The ITI was approximately 2–4 min. Each day contained an equal number of forced right or left turns in a pseudorandom sequence.

**Acquisition: One maze (Sessions 1–20)**

All rats received 20 sessions, each session containing eight trials. The interval between the end of the forced sample run and the start of the choice run was typically 3 s. Only two trial types were used, and these were the same as Trial Types 1 and 4 from Probe I of Experiment 1 (see Figure 1). These two trial types were selected because when they are given in equal numbers the benefits afforded by place and intramaze cues should be nullified. Direction cues will, however, aid Probe Type 1 and need not affect Probe Type 4. These two trial types and the start arms used were counterbalanced and were presented in a pseudorandom sequence. When possible (Probe Type 1) the correct arm for the choice phase was prebaited before both components of the trial.

**Two-maze learning (Sessions 21–60)**

In order to remove all intramaze cues, different mazes were used for the forced and choice runs. The two adjacent cross-mazes (initially in the same room and general location as the original maze) were used for all of the remaining sessions (21–75). For the first 16 sessions in the two mazes (Sessions 21–36) the rats received eight trials per session. In order to encourage the use of egocentric cues the time between the end of the forced and choice runs was minimized (to typically 2–3 s). For this reason, training used only the same arm combinations as those described for the two-maze condition in Experiment 1 (Figure 3). This resulted in eight trial conditions (the four
basic types shown in Figure 3, which could start from either the north or the south arm). The order in which the mazes were used was counterbalanced, with the forced turn always starting from either the north or the south arm of one maze and the choice run starting from one of two possible arms in the other maze. For Sessions 37–48 the rats received 12 trials per session, but returned to 8 trials per session for the final 12 sessions (49–60).

**Room transfer (Sessions 61–66)**
For six sessions (Sessions 61–66) rats were tested in a completely different test room. This was carried out to examine the possibility that although the experiment was run under low light levels the rats had gradually learnt polarizing features about the room in which they were trained. Both mazes were removed to the new room, which differed only slightly in dimensions (301 × 280 × 255 cm). The two mazes were placed again in the middle of the room side by side and the same distance apart as that in the previous room. Trials were identical to the previous two-maze learning sessions.

**10-s delay (Sessions 68–73)**
Rats received a standard two-maze training session in the original test room (Session 67) followed by six sessions to investigate the effect of increased retention intervals. Using exactly the same procedure as that followed for the two-maze learning task, the rats received six sessions (Sessions 68–73) in which a delay of 10 s was presented between the forced turn and the choice run in a pseudorandom sequence, intermixed with standard trials. That is, for the eight trials per session each rat received four delay trials and four standard trials in a pseudorandom order. For all the delay trials the rat was placed immediately into the start arm for the choice run. The rat was then held in the start area for 10 s by a barrier preventing the rat from moving down the arm to the choice point. After the 10-s delay period the barrier was removed, and the rats were allowed to run the maze.

**Retest: No delays**
Rats were tested for a final two sessions (74–75), using exactly the same procedure as that used for the last 10 sessions of the two-maze condition (i.e., the interval between the end of the sample run and the start of the choice run was reduced to 2–3 s).

**Results**

**Spontaneous locomotor activity**
Long-Evans rats were more active than Dark Agouti rats (see Figure 9) as measured by the total number of beam crossings, $F(1, 28) = 25.72, p < .001$. This strain difference remained stable across the two test sessions.

**Acquisition (one maze)**
The rats acquired the nonmatching rule (see Figure 10), as shown by the comparison between the first 10 and the second 10 acquisition sessions, $F(1, 318) = 5.67, p < .05$. Even so, performance on the last block of two sessions only averaged 63%. An ANOVA found no effect of strain, $F(1, 140) = 3.25, p > .05$, and no block by strain interaction ($F < 1$). Overall performance for all sessions was significantly above chance for Dark Agouti (56.1%), $t(7) = 3.39, p = .01$, and for Long-Evans (58.8%), $t(7) = 5.98, p < .001$, rats. Examining all the acquisition sessions for the two separate trial types showed that performance
on Trial Type 1 (mean = 61%) was better than that on Trial Type 4 (mean = 54%), and the two trial types (Figure 10) differed significantly, $F(1, 636) = 20.29$, $p < .001$. Trial Type 1 was the arrangement that would have permitted the use of direction cues to solve the problem. There was no strain by trial type interaction, $F(1, 636) = 1.90$, $p = .17$.

Testing with two mazes
In order to remove intramaze cues the remaining conditions used different mazes for the sample and the choice run. Overall performance (Sessions 21–60) across the four trial types (Figure 11) remained significantly above chance, $t(15) = 8.41$, $p < .001$, mean 63%. Across all two-maze trials there was no difference in performance between the two strains ($F < 1$). Over the first 16 sessions of two-maze learning (Sessions 21–36), performance remained stable, and there was no effect of session, $F(5, 360) = 1.12$, $p > .1$, Figure 11 (left). Increasing the number of trials from 8 to 12 (Sessions 37–48) resulted in an initial decrease in performance: last block 8 trials versus first block 12 trials, $F(1, 636) = 5.95$, $p < .05$. Nevertheless, overall performance did not differ between 8 or 12 trials per session, $F(1, 37) = 3.41$, $p > .05$.

It was once again found (Sessions 21–60) that trials having the same direction for the sample and the choice run (Trials A and B) had higher accuracy than trials where the direction differed for the sample and choice run (Trials C and D). However, although performance levels differed between the two categories of trial (A and B higher than C and D), performance on all trial types was significantly above chance: A, 73%, $t(239) = 10.92$, $p < .001$; B, 69%, $t(239) = 10.75$, $p < .001$; C, 59%, $t(239) = 9.14$, $p < .001$; D, 61%, $t(239) = 7.20$, $p < .001$. This ranking is identical to that found in Experiment 1, where DA rats obtained very similar levels of performance, but now all trial types were significantly above chance.
Room transfer
Performance showed a transient drop lasting up to 4 days when testing was moved to a novel room. Performance did, however, increase following this disruption, session, \( F(5, 84) = 4.46, p = .001 \), to a level comparable to that prior to room transfer. There was no effect of strain \( (F < 1) \) and no strain by session interaction \( (F < 1) \).

Delay 10 s
There was no effect of strain over the six sessions \( (F < 1) \). There was, however, a significant effect of trial type as performance was higher for standard trials than for the delay trials, \( F(1, 30) = 4.23, p < .05 \) (Figure 12). Analysing the two trial types separately showed that only the standard trials were performed above chance: DA, 62%, \( t(7) = 3.21, p = .01 \); LE, 64%, \( t(7) = 3.69, p < .01 \), whereas the 10-s delay trials did not differ from chance: DA, 55%, \( t(7) = 1.57, p = .16 \); LE, 54%, \( t(7) = 0.59, p = .57 \).

Retest: No delays
All rats finally received two sessions, exactly the same as in the previous stage except that there was no additional delay. Now performance was significantly above chance: DA, 63%, \( t(7) = 2.37, p < .05 \); LE, 64%, \( t(7) = 2.61, p < .05 \).

**GENERAL DISCUSSION**

The principal goal of the present study was to examine how different spatial strategies interact.
in an alternation task where only particular cue types (egocentric and idiothetic) consistently predict the correct choice. The extent to which other cues could support responding was manipulated by using different sets of arms for the sample and choice runs. These manipulations included rotating the maze within trials and using two separate mazes to remove intramaze cues. A consistent finding was the difficulty that rats had in using either egocentric or idiothetic working memory. Experiment 1 showed that avoiding recently visited places and recent intramaze cues largely dominated performance, so much so that for some conditions performance was significantly below chance when both of these cue types opposed the correct choice (e.g., Probe I, Types 3 and 4, Experiment 1). Only after extended training using two mazes did evidence for successful alternation behaviour emerge. Even then, performance was poor with scores around 60% in Experiment 1 and around 64% in Experiment 2. In these conditions other cue types were excluded (intramaze, direction) or set in opposition to cancel each other out across trials (place). Even so, this form of working memory appeared to be very fragile. Thus, when an additional delay of 10 s was added from the end of the sample run to the start of the choice run performance fell to chance levels. This same pattern of results was observed in two different strains of rats (Dark Agouti and Long-Evans), showing the generality of this finding.

Both experiments indicated that rats can use a set heading direction to alternate around (Douglas, 1966; Dudchenko & Davidson, 2002). This was easiest to demonstrate in the two-maze condition, where similar results were found for both experiments. Some previous experiments have also used a two-maze arrangement to examine direction cues but, with the exception of Dudchenko and Davidson (2002), these previous investigations have studied spontaneous alternation (e.g., Douglas, 1966; Lester, 1968; Potegal, Day, & Abraham, 1977; Still & MacMillan, 1969) rather than forced choice. The present results with forced-choice alternation, therefore, add to the generality of the finding that rats can effectively use direction cues. While a change in orientation by 90° between sample and choice led to a loss of this direction cue (Douglas, 1966; Dudchenko & Davidson, 2002; Lester, 1968), a change by a further 90° (so that the sample and choice runs now began in directly opposite directions) did not seem to yield an additional impairment. This result comes from the finding that Probe 4 was no more difficult than Probe 3 (see Figure 5); that is, direction cues either aided or were neutral. Dudchenko (2001) also found evidence that a rotation of 180° does not result in a further level of difficulty over 90°. The original discovery that heading direction could be used as a basis for alternation (Douglas, 1966) accords with the subsequent discovery of “head direction cells” (Ranck, 1984; Taube, 1998), which might provide part of the information required for this form of alternation. This link may help to explain why lesions in brain sites that contain head direction cells are associated with alternation deficits (Aggleton et al., 1995; Béragochea & Jaffard, 1994, 1995; Vann & Aggleton, 2004). These findings also point to the importance of vestibular cues for alternation (Brown & Moore, 1997; Potegal et al., 1977; Smith, 1997) as this information can contribute to head direction tuning (Taube, 1998). At the same time, direction alternation does not provide a sufficient account of the rats’ behaviour as performance on three of the rotation probes (1, 3, 6) was significantly above chance even though direction cues should not aid accuracy.

At least five strategies could support T-maze alternation: avoidance of familiar place, avoidance of familiar intramaze cues, alternation of direction, egocentric alternation, and idiothetic alternation (i.e., nonmatching-to-turn). It was possible to predict the overall ranking of performance levels in the present experiment simply by assuming that the effects of place and intramaze cues could be added or subtracted, while direction cues could be added but not subtracted (i.e., treated as neutral if choice and sample runs are not aligned). These assumptions led to a correct, qualitative prediction of the performance levels in Probe I of Experiment 1. The next condition,
rotation probes, was more complex, and while many of the results fitted this predicted ranking there appeared to be divisions with the effects of place and intramaze cues. Notably, rats most clearly avoided the arm in the location of the start arm (Rotations 2 and 7), and rats avoided the intramaze cues associated with the arm in which they were fed on the sample run. It is also the case that performance on Rotation Probe 6 was higher than predicted (see Figure 6), and we have no explanation for this specific result at present. Data from the two-maze conditions in Experiment 1 and 2 could also be considered within this framework. The only departure from the prediction that the accuracy of the trial types should be in the rank order \( A = B > D > C \) was that the scores for Trial Types D and C did not differ significantly. It was, however, the case that in both experiments Condition C had the lowest overall scores. Finally, the initial acquisition stage of Experiment 2 used two different trial types, and, as expected from the cue disposition, performance on those trials matching Probe Type 1 of Experiment 1 was superior to that matching Probe Type 4. In predicting these rankings any contribution from egocentric or idiothetic working memory was ignored as this should be constant across the trial types.

In their hugely influential analysis of hippocampal function and spatial learning, O'Keefe and Nadel (1978) proposed two different mechanisms to support navigation: the taxon and locale systems. The taxon system was thought to rely on a combination of egocentric and idiothetic information, and it is this hypothetical system that should support nonmatching-to-turn behaviour. The difficulty that rats had in performing an egocentric/idiothetic alternation task and its apparent transience accords with the prediction that the taxon system suffers from high interference (O'Keefe & Nadel, 1978, p. 100). For this reason, such cues should be ineffective for working memory tasks in which information from previous trials must be distinguished. This may explain why performance initially decreased when the numbers of trials per session were increased from 8 to 12 in Experiment 2. Consistent with the predictions of O'Keefe and Nadel (1978) other studies have found that body turn or egocentric working memory are of very restricted use. This evidence comes from analyses of spontaneous response alternation (Douglas, 1966; Estes & Schoeffler, 1955; Restle, 1957; Walker, Dember, Earl, & Karoly, 1955) and the difficulty of training rats on a nonmatching-to-turn rule (Baird et al., 2004). While acquiring a nonmatching-to-turn rule in a radial-arm maze proved ineffective it was, however, possible to achieve relatively high rates of nonmatching in a J-shaped maze (Baird et al., 2004). The J-maze made it possible to train rats with short intervals between the sample and choice turns (approximately 3 s), and the rats were not handled within a trial (Baird et al., 2004). Both of these features were included to minimize proactive interference. Once again though, the addition of short, additional delays (3 s) caused performance to fall to chance levels.

In spite of the difficulty that rats can have in nonmatching using idiothetic or egocentric cues (Baird et al., 2004; Restle, 1957), a number of studies have trained rats on matching tasks in which they have achieved much higher accuracy rates than those in the present experiment; with performance levels well above chance even after retention delays of over 30 s (Kesner, Bolland, & Dakis, 1993; Kesner et al., 1996; Ragozzino & Kesner, 2001; Rasmussen et al., 1989). For some of these studies the rats were trained in the dark to help eliminate distal cues (Ragozzino & Kesner, 2001), while in other studies the relative positions of the choice arms were designed to nullify the use of place cues (Kesner et al., 1996; Rasmussen et al., 1989). Careful analysis of these tasks suggests, however, that some of these high scores may reflect a failure to exclude the use of intramaze cues and directional cues (Baird et al., 2004; Dudchenko, 2001). In the study by Ragozzino and Kesner (2001) rats could use intramaze cues in a cross-maze to make a correct choice, and the present study reinforces the likelihood that this would be an effective strategy. A radial-arm maze was used by Rasmussen et al.
(1989) who trained rats on a nonmatching-to-turn task. Intramaze and location cues were nullified by the selection of the arms used for the sample and choice runs, but the procedure meant that the correct arm on the choice run was always directly opposite the arm used at the start of the choice run—that is, by maintaining the original direction the task could be solved. For this reason an alternative strategy may have been used. A third task used the top three arms of a maze for the sample turn and the bottom three arms to test the choice turn (Kesner et al., 1993, 1996). Long-Evans rats were trained on a matching-to-turn rule and, although requiring a mean of 650 trials to reach a 75% criterion (Kesner et al., 1996), were able to perform appreciably above chance with delays as long as 30 s. A potential problem with this design is that the correct choice is always in the location that is furthest away from the location used for the sample run. It is not possible to determine whether any rats used this opposite location strategy, but this design feature reveals again how difficult it is to produce an egocentric working memory task that is not soluble by other means.

In contrast, rats seemed much more adept at using intramaze cues. It was found that rats alternated away from the actual arms that they had already traversed or entered within that trial. Evidence for this use of intramaze cues came from the rotation probes (e.g., Probes 1–4 vs. Probes 5–8). It is not possible to define what type of cue the animals were using, but the very low illumination makes it most unlikely that they could have used visual cues. Furthermore, attempts to provide visual or tactile intramaze cues to aid alternation have shown that rats are poor at using such cues (Douglas, 1966) unless they are very distinct (e.g., black arm vs. white arm; Walker et al., 1955). This leaves olfactory cues as a likely candidate, and previous studies have shown that scent trails can aid alternation (Douglas, 1966; Wallace, Gorny, & Whishaw, 2002; but see Still & MacMillan, 1969). Indeed, in some experiments scent trails are sufficient to account for all intramaze effects (Douglas, 1966). In the present study this intramaze cue usage was presumably aided by the deliberate decision not to wash the maze between runs. Evidence was also found that rats show a stronger aversion to an arm in which they have recently eaten, as compared to arms that have merely been traversed to reach food. This is an intriguing difference, which may be related to the finding that rats are more reluctant to re-enter an arm where the food supply has been exhausted than one in which the food was only partially depleted (Gaffan & Eacott, 1986). This comparison is, however, confounded by the relative recency of the two arms and so warrants further investigation.

The rats in the present experiment had a strong bias to avoid entering an arm that was in a location that they had already entered. It should be remembered that all of the experiments were run in very low light levels and the maze had high, opaque walls. It is, therefore, most unlikely that location was defined by distal allocentric, visual cues. One possibility is that the rats had learnt the geometric arrangement of the maze and that this information, combined with vestibular feedback associated with being moved between the sample and choice phases, allowed the rat to determine when it was re-entering the same place. Support for this interpretation comes from the finding that rats can perform radial-arm maze working memory tasks when visual extramaze cues are removed, and intramaze cues are controlled (Brown & Moore, 1997). Likewise, blind rats are able to perform the standard radial-arm maze task to a high degree of accuracy (Zoladek & Roberts, 1978). Dudchenko (2001) also found that extramaze cues were not required for accurate T-maze alternation, even when intramaze and direction cues had been removed or nullified. Nevertheless, some awareness of the room identity was shown by the room switch condition (Experiment 2), which also showed that rates of egocentric/idiothetic alternation were not specific to a given room as they rapidly recovered.

An intriguing problem with the two-maze design used in Experiments 1 and 2 is how to assign place cue effects. Figure 3 assumes that the rats treat the two mazes as if they were just one and, hence, are in the same location. In
fact, the rats could treat them as two separate mazes that are placed side by side. The key test of these two different assumptions is the comparison between Trial Types A and B (see Figure 3). If rats appreciate that they have been moved to one side (i.e., two mazes) then Trial A should be more difficult than B, as in Trial A rats run towards the same location on the sample and choice runs but in Trial B the rats run away from the sample location. The lack of a superiority for B over A (in fact, in both experiments A was slightly better than B) argues strongly against the latter view. There is, however, a third possibility. This is that rats learn that they are sequentially placed in two mazes set in different locations that never overlap, so there is no reluctance to converge towards the same location (Trial Type A). We cannot yet exclude this final possibility.

The rationale for these studies arose from the increasing use of forced-choice alternation in neuroscientific investigations of spatial working memory. The present results highlight a paradox that has already been noted by Dudchenko (2001). The discovery that multiple strategies can support T-maze alternation means that a lesion that affects a single strategy should not reduce performance to chance levels. It is, however, the case that lesions of the hippocampus (Aggleton, Hunt, & Rawlins, 1986; Dudchenko et al., 2000) and medial thalamic nuclei (Warburton & Aggleton, 1999) can result in chance level performance. This suggests that a structure such as the hippocampus is necessary for more than one strategy (Whishaw, 1998), or that the loss of one strategy blocks the use of another strategy (i.e., they are not independent). The latter view (mutual dependence) seems most unlikely, however, given the effects of the various probes, which reveal how cue effects can summate and do not seem mutually dependent. Consistent with this conclusion is the finding that the removal of cue types (e.g., distinct visual extramaze cues), can seemingly leave T-maze alternation unaffected (Liu & Bilkey, 1998). The implication is that these brain regions are important for more than just one form of spatial strategy. In summary, the results support the “multiple cue” theory of Restle (1957) as not only are there multiple cues types available for spatial learning but rats will flexibly switch between cue types as one or more are removed. Within this hierarchy, idiothetic and egocentric cues seem to be the least readily available for working memory tasks.

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