

# Heading in the rat: Determination by environmental shape

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After a 75-sec intratrial delay, rats that had been shown the location of hidden food within a rectangular box correctly dug at that location in a second identical box, which had been moved into the same position within the room. For some rats, the opposing ends of the boxes were differentiated by distinctive corner panels; for others, there were no panels. When, during the delay interval, the turntable supporting both boxes was rotated by more than 180°, so that the second box no longer took the place of the first box within the room, the rats showed performance decrements. Nevertheless, 4 subjects selected the correct location significantly more often than the rotationally equivalent location, which corresponds to the correct location when the ends of the box are confused. The amount of rotation had no significant effect for any rat. In a final phase, the rats were denied perceptual access to cues outside the test box, which now had differentiating corner panels for all rats. Despite the distinctive panels, no rat showed a significant difference between correct digs and rotational errors; that is, no rat reliably distinguished one end of the box from the other. Results confirm previous findings that rats rely primarily on environmental shape to establish their heading. They ignore distinctive features of the surfaces that define environmental shape, even when the shape by itself is insufficient to establish a unique orientation.

Recent experiments have strengthened the longstanding hypothesis that diverse animals form cognitive maps, behaviorally useful records of the geometric relationships among points in the environment (Gould, 1986; Tolman, 1948). Animals commonly orient toward points that are specified not by their intrinsic sensory/perceptual characteristics but rather by their remembered location within the spatial framework defined by surrounding objects (Tinbergen & Kruyt, 1938; Tinklepaugh, 1932; see Gallistel, 1989, for review of recent literature). This form of animal orientation is sometimes called piloting, by analogy to the orienting of mariners with respect to a hidden shoal on the basis of the shoal's remembered (charted) location relative to observable shore points. The experiments of Morris (1981) with rats in a water maze make this analogy particularly apt: The rats were to find a brick just beneath the surface of opacified water. The hidden brick itself had no distinctive features; thus, it had to be found by virtue of its position within the known space (the swimming pool and the experimental room).

Establishing one's position and orientation (heading) within the framework established by the known (mapped) aspects of the environment is fundamental to piloting. There is extensive experimental evidence that extramaze, or "room," cues are important determinants of the rat's orientation within a maze (Carr, 1917; Hebb, 1938; Olton & Samuelson, 1976; Ritchie, 1947; Suzuki, Augerinos, & Black, 1980), but what constitutes the behaviorally im-

portant components of the extramaze environment remains to be determined. Cheng (1986) reports results suggesting that, in determining its heading within a familiar environment, the rat relies on its perception of the macroscopic shape of the environment, which is defined by the relative positions of surrounding surfaces. Under Cheng's conditions, the rats ignored distinctive features of the surfaces themselves (blackness vs. whiteness, patterns of pin-hole lights, textures, odors, etc.). We now report experiments further testing the hypothesis that in establishing its heading the rat relies primarily on the macroscopic shape of the environment.

In the experiments that most directly inspired our own, Cheng (1986) showed rats the location of a dish of food within a rectangular box, with the location chosen randomly for every trial. When a rat had eaten a few pellets from the dish, Cheng removed it from the box for 75 sec, then returned it to an identical box with food buried in the same place. The rat's task was to dig out the food in the second box. This second box was used to prevent the rat from marking the location of the food with an odor. The rat was removed from the first box and returned to the second in total darkness, in an attempt (only partially successful) to disrupt its inertial reckoning of its heading. In addition, the boxes were rotated by randomly varying amounts, between trials and during the 75-sec intratrial delay. These measures were designed to force the rat to establish its heading by reference only to the experimental boxes themselves.

There is evidence that, unless measures are taken to disorient them, rodents retain knowledge of their orientation with respect to the larger room (their global head-

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ing), even when it is no longer immediately perceivable (Carr, 1917; Mittelstaedt & Mittelstaedt, 1980; Potegal, 1982). They do this by angular "dead reckoning," that is, by keeping track of how much they have rotated since losing perceptual contact with the surfaces that define the larger space. When out of direct perceptual contact with the global environment, they maintain the sense of their global heading by integrating their angular velocity with respect to time to obtain their current angular position. To disorient them with respect to the global environment, one must defeat this angular dead-reckoning process by slow and sustained rotations in the dark (see Mittelstaedt & Mittelstaedt, 1980).

In Cheng's experiments, four panels, one in each corner of the rectangular box, were intended to serve as landmarks that distinguished one end of a box from the other. The panels differed one from another in pinhole light pattern, smell, brightness, and texture. In addition, one of the two long side walls was white Styrofoam, while the opposing side wall and the two end walls were black (painted) plywood. When the rat faced the 120×35-cm Styrofoam wall, the bright white sheet nearly filled its visual field. Despite these salient differentiating features of the enclosure's surfaces, Cheng's rats were often misoriented. About 80% of the time, they dug at locations bearing the correct geometric relationship to the space defined by the shape of the rectangular box, but approximately half of all such digs were at the rotational equivalent of the food's correct location.

The rotational equivalent to a given location in a rectangular box is the location into which the given location would move if the floor of the box were rotated by 180°. This location is indistinguishable from the given location unless one end (or side) of the box is distinguished from the opposite end (or side). If the rat failed to take into account the white-black distinction between opposing sides, and the smells and other features that distinguished each corner from every other, then the rotationally equivalent location was bound to be confused with the correct location half of the time. There is no way to distinguish the two ends of a rectangular box on the basis of its shape alone, because the rectangular shape is congruent with itself when rotated 180°. In Cheng's experiments, the rats appeared to determine their heading solely on the basis of the macroscopic shape of the perceivable environment; hence, they were misoriented by 180° on half of the trials.

The same rats would use the same corner panels as "flags," marking the position of food, when the food was in front of the same panel from trial to trial (cf. Morris, 1981). However, when the flags in the correct corner and its diagonally opposing rotational equivalent were removed, the rats dug in the rotational equivalent of the correct corner on half of the trials, despite the fact that the distinctive panels that remained in the two corners on the other diagonal of the rectangle distinguished one end of the box from the other as much as did the panels removed from the correct corner and its rotational equivalent. A flag is an object or feature that is used to single out some point in the environment, but which does not serve to es-

tablish a heading (orientation) with respect to the space as a whole. In Cheng's experiments, the corner panels served as flags that marked the location of the food, but they did not serve to establish the animal's heading (i.e., how it was oriented within the box).

Our experiments were designed, first, to test Cheng's assumption that the rotational confusions he observed depended on the rat's being disoriented or misoriented with respect to the space outside the box (the extramaze environment). All of Cheng's experiments were run under conditions designed to attenuate the rat's sense of its heading with respect to the extramaze environment, and all of Cheng's rats showed rotational confusions.

Second, our experiments were designed to test the hypothesis that when a smaller, geometrically polarizing environment (the table containing the two boxes) was rotated within a larger environment (the room), the animals would react to this rotation, but they would, nonetheless, be able to take their heading from the smaller framework. An environment is said to be geometrically polarizing if its shape alone defines a unique orientation within the polarized space. The locations of our test and exposure boxes on the tabletop geometrically polarized them, because one side wall of each box was toward the outside of the circle and the opposite side wall was toward the center (see Figure 1).

Finally, we tested one explanation for the puzzling fact that Cheng's rats failed to take their heading from the distinctive features of the corner panels and side walls. Perhaps the rats failed to take their headings from these

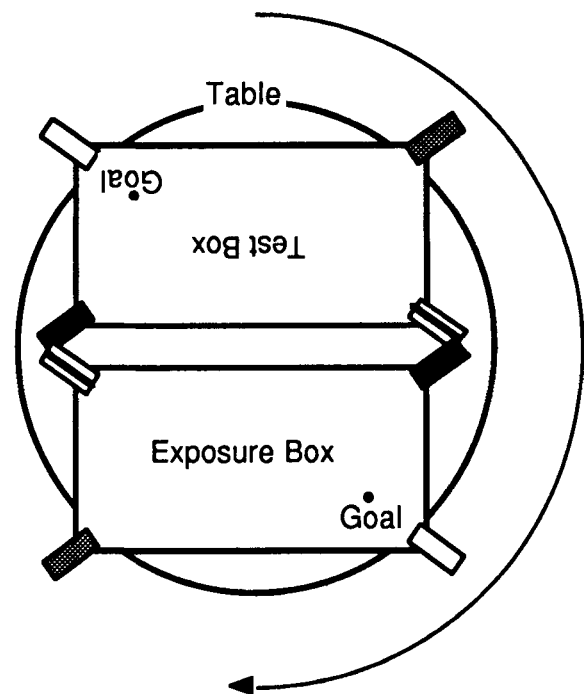


Figure 1. Schematic representation of experimental apparatus. (Panels pertain to Group 2 only.) Note that when tabletop is rotated 180°, the panels and the goal in the test box move into the locations occupied by the corresponding panels and goal in the exposure box.

distinctive features of the enclosing surfaces because, in their experience, these features changed location within the box. If, on being placed in the familiar box, the rat tried to compute its heading from the rectangular shape alone, it would be misoriented by 180° half of the time. At such times, the rat might perceive the corner panels and white Styrofoam sheet as being in the "wrong" places. That is, it might experience these distinctive features of the surfaces as having changed their locations within the box. No larger perceptual frame of reference was available to prevent such a misconception by revealing that the box itself had rotated. We reasoned that if a larger perceptual framework were provided, the rat might discern that the positions of the distinctive panels within the box were fixed; it would then learn to use these corner panels to disambiguate opposite directions within the box.

Experiment 1 was run with the same boxes and nearly the same protocol as Cheng used, but in a normally lighted experimental room. Both the shape of the experimental room and the location of a box relative to the tabletop provided a purely geometric basis for determining a unique orientation within a box itself. The purpose was to demonstrate that, under these conditions, rats do not show rotational confusions. Their sense of their heading within the extramaze environment prevents them from being misoriented within the box.

One group of rats was run with no corner panels; a second group was run with distinctive panels in corners. These two groups continued into Experiment 2, which was a continuation of Experiment 1, except that in Experiment 2 a box changed its position and orientation within the room during the intratrial delay. The rats run with distinctive panels in the corners had the opportunity to observe that these panels remained fixed within the box when the box itself changed its position and orientation within the room.

The same rats continued in Experiment 3, which was run under Cheng's conditions: The rats were unoriented with respect to the extramaze environment, but there were distinctive panels in the corners for both groups of rats. The performances of rats with and without prior panel experience could then be compared.

## EXPERIMENT 1

### Method

**Subjects.** Ten male Sprague-Dawley rats received training. At the outset, the rats were 2½ months old and experimentally naive. For the first 2 months of training, they had free access to food and water. After that, lab chow was available only from 2:00 p.m. to 4:00 p.m. each day. In the test phase, daily sessions started 2½ h into the dark phase of the rats' light:dark cycle (at 9:30 a.m.).

**Apparatus.** Two rectangular boxes (120×60 cm, with walls 35 cm high) were arranged on a plywood turntable 1.65 m in diameter, so that the boxes' longer sides were parallel (Figure 1). The inner surfaces of the walls were painted semiglossy black. The bottoms of the boxes were covered with a 9-cm-high layer of Pine-Dri bedding. On the floor beneath the bedding of each box, nine lines parallel to the box's short walls and nine lines parallel to the

long walls formed a concealed grid, which divided the floor into 100 12×6-cm rectangles.

For half of the rats, distinctive panels fit snugly into each box corner, forming an angle of 30° with the long wall and 60° with the short. Each panel was 11 cm wide, 33 cm high, and 3.3 mm thick. Panels were distinctive in texture and visual markings: two were Masonite—one painted glossy black and the other flat white; a third was aluminum; the fourth was white foam-core with a 2-cm-wide strip of black tape running down its center. The panel arrangement (which panel should be assigned to which corner) was chosen randomly for each rat, but held constant for that animal.

In training, the food was in a glass ashtray (9 cm square and 2 cm deep) on the floor of the box, at a grid intersection. In test, the dish (ashtray) and food were replaced by a black plastic checker (3 cm in diameter and 5 mm thick), because there was evidence that some rats could sniff out the buried food. Thus, during the data-collecting phases of Experiment 1 and the subsequent two experiments, the presentation of the (odoriferous) Cocoa Puffs was paired with the finding of the (odorless) checker, making the checker a conditioned reinforcer.

The entire apparatus was centered in a brightly lit room (3.6×3.4 m). The racked cages where the rats awaited their trials stood beside the door. The separate cage into which each rat was placed during its session's delay interval was located against an adjacent wall.

**Procedure.** During the first 2 weeks, each rat was handled for 5 min a day. Over the next 10 days, each rat spent 10 min daily in one of the two boxes, with seven Cocoa Puffs available in the dish at a random grid location. The rats then received 10 training trials, one a day, with the food partially buried at the same grid location in both boxes. The 10 locations (among 80 possible) were chosen randomly for each rat, with the following two constraints: the box center (grid point 5,5) was excluded as a food location and adjacent locations were avoided on any 2 consecutive days. Seven Cocoa Puffs were in the food dish in the exposure box, four in the test box. The bedding was level in both boxes except where the food was located; in these spots, the bedding was scooped out so that only a very thin layer covered the dish.

A rat first was placed in the exposure box, to find and eat the pellets. If it hadn't eaten within 2 min, the dish was completely exposed. The rat was removed after eating a third pellet and placed in a separate cage for the 75-sec intratrial delay. Although this waiting cage faced the apparatus, the rats did not regularly orient toward the apparatus or appear to observe what was done. During this period, the tabletop was rotated 180°, so that the test box, which was identical in every respect to the exposure box, occupied the location previously occupied by the exposure box. It was our intent that the rats perceive the test and exposure boxes as one and the same. So far as we could judge, they did. In the test box, the rat had 2 min to find the pellets. After that, the food was completely uncovered, and the rat was allowed to eat all of it.

In the second phase, of 18 trials (two daily, the first at 9:00 a.m., the second at 4:00 p.m.), the food was completely buried in both boxes, to see whether the rats could sniff out the food. Since there was evidence that at last some of the rats could discern the food's location by smell, we decided to switch from buried food to a buried plastic token (odorless conditioned reinforcer), but only after the rats' success at finding the primary reinforcer (the food itself) had reached asymptote.

In the third phase of training, the food was barely covered in the exposure box but completely buried in the test box. On entering a box, the rat was positioned at either (1) the middle of a wall, facing the box's center or (2) the center, facing the middle of a wall. Whether the entrance location was center or wall was decided randomly, as was which wall would be faced or touched. The only constraint on randomization was that each rat's entrance position differed on any two consecutive box entrances (whether intertrial or intratrial). For 2 months, the rats were run one trial daily (9:30

a. m.). When the 10 rats' performance appeared to have stabilized, 3 rats were dropped from the experiment because they had failed to demonstrate an understanding of the task: 2 rats wouldn't dig and another rat dug almost exclusively at corners. At this point, the test phase began.

The performance of the 7 rats that entered the test phase of Experiment 1 remained at asymptote throughout the 5 weeks of the test phase, although the procedure was changed to the use of the token at the beginning of this phase. No food was buried in either box—only a plastic checker. On each trial, the rat was placed in the exposure box and given 2 min to dig at the token location; if it hadn't done so within 2 min, the token was revealed. A small container (3 cm in diameter at its base, 3.3 cm high, and 4.4 cm in diameter at its top rim) holding seven Cocoa Puffs was immediately placed on top of the token. Each rat was removed after it had eaten three pellets, and was placed in the waiting cage for 75 sec. The rat then was placed in the test box (which had been rotated into the location of the exposure box), where it has 2 min to dig for the token. If it hadn't dug within this time, the token was uncovered and the container with four Cocoa Puffs was placed on top of it. A *dig* was operationally defined as the first scratching of bedding at a localized area. Sticking the nose just under the surface or running around with the head under the surface did not count. The dig location was taken as the center of the dig's deepest part, recorded to the nearest half unit on both axes of the floor grid (3 cm on the short axis, 6 cm on the long axis).

## Results

Dig locations were classified into one of three categories—those used by Cheng (1986). If a dig was within 15 cm of the center of the target location, it was correct. If it was within 15 cm of the rotationally equivalent location (the location assumed by the token after an imagined 180° rotation of the rectangular box), it was a rotational error. Other errors were called misses (Table 1).

Each animal's performance was individually analyzed. A circle of 15 cm radius covers 10% of the box's surface area. Chance correct performance would, therefore, be 10% of the 35 trials, or 3.5 correct digs. The number of correct digs for each of the 7 rats far exceeded this. In every case, the binomial probability of attaining such high performance by chance was effectively zero. By contrast, binomial tests showed that no rat made significantly more than the expected number of rotational errors ( $p > .05$ , in all seven cases). One rat (JM2) showed a

significant tendency to make corner errors (binomial  $p = .02$ ).

Increasing or decreasing the radius within which digs were scored as correct had commensurate effects on the percentage of correct scores. The choice of a radius did not alter the pattern of results, in Experiment 1 and the subsequent experiments.

There was no significant effect of the panels on the percent correct digs [ $t$ -test comparison of the mean number correct for Group 1 (no feature panels) vs. Group 2 (panels)].

## Discussion

Cheng's (1986) rats showed no statistically significant difference between correct digs and rotational errors, but our rats did not make significantly more rotational errors than expected by chance. The performance of rats run without panels was as free from rotational errors as the performance of rats provided with such panels. It therefore seemed probable that all rats got their headings from extramaze cues, whether or not they had panels differentiating one end of the box from the other.

## EXPERIMENT 2

Experiment 2 was in most respects a continuation of Experiment 1. The only difference was that the tabletop was not rotated to position the test box in the location previously occupied by the exposure box; rather, it was rotated so that the location of the test box differed in both position and orientation from the location occupied by the exposure box. The location and orientation of the test box was chosen randomly from among the sequence of locations generated by rotating the tabletop in 30° increments away from its position during the exposure phase of a trial, omitting only the 180° rotation that carried the test box into the location occupied by the exposure box. There was one constraint on the random selection of locations for the test box: for each rat, no location was repeated on 2 consecutive days. The rats were run one trial per day, for 40 days.

One purpose of Experiment 2 was to confirm that the rats had oriented by means of large-scale room cues in Experiment 1. A second purpose was to determine whether the rats could learn to take their orientation from the more local geometry (the tabletop) and/or from the intramaze cues (the corner panels). A third purpose was to demonstrate to the rats in Group 2 (the rats run with corner panels) that the panels had a fixed location in the box, a location that did not vary when the location of the box within the room varied.

## Results

In the group with corner panels, 1 rat (JM7) dug correctly on the first day of Experiment 2, dug at the rotational error on the second day, and thereafter didn't dig at all. Because it had been among the best performers in Experiment 1, its refusal to dig in a test box that had changed its position and orientation within the room was

Table 1  
Percent Digs (Out of 35 Digs) at Correct, Rotationally Equivalent, and Incorrect Locations in Experiment 1

Rats	% Correct	% Rotational Errors	% Misses	% Corner Errors
JM1 (N)	89†	6	6	3
JM2 (N)	60†	3	37	23*
JM3 (N)	66†	6	29	6
JM4 (N)	74†	9	17	0
JM5 (P)	91†	0	9	0
JM6 (P)	80†	6	14	6
JM7 (P)	91†	0	9	0
Mean	79	4	17	

Note—A corner error also could have been a rotational error or a miss; therefore, the Corner Errors category does not exclude the other types of errors. N = no panels; P = panels. \* $p < .05$ , † $p < .001$ , binomial likelihood that the proportion would be this great or greater.

a dramatic manifestation of the importance of the extramaze environment in determining a rat's orientation within a maze, even when the surfaces that enclose the maze have distinctive markings from which the rat could determine a unique orientation within the maze.

In the group without corner panels, the rat JM2, which showed a slight tendency to dig in the corners in Experiment 1, now made corner errors on 24 of 40 trials ( $p < .001$ , binomial probability). Its number of correct digs was only 8, which is not significantly greater than the chance expectation (4). Thus, 2 of the 7 subjects that progressed to Experiment 2 did not learn to use more local properties of the environment to orient themselves within the box, or, at least, they were so enduringly perturbed by the varying relation between the test box and the room that they did not continue to show a statistically significant tendency to dig at the location of the token.

The other 5 rats continued to show a highly significant tendency to dig at the correct location (binomial  $p < .005$ , or less), although there was in every case a substantial drop in the percentage of correct digs (see Table 2). A paired comparison  $t$  test for the percentage correct digs in Experiment 1 versus the percentage correct in Experiment 2 for the 5 rats (whose data are given in Table 2) yields  $p < .01$ . Thus, the change in the position and orientation of the test box relative to the room had a strong negative impact on the performance of the group.

Of the 5 rats that continued to show a significant tendency to dig at the correct position, all but JM3 showed a significant difference between the number of correct digs and the number of rotational errors (in all four cases,  $p < .01$ , by chi-square test). We also used the chi-square test to check whether there was an effect of the amount of rotation upon the tendency to dig correctly. No rat showed a significant effect of amount of rotation on either number of correct digs or number of rotational errors. Nor did any rat show a significant tendency to improve over time. The implication is that the rats stuck to whatever strategy they adopted at the beginning of this experiment, when they first encountered a test box that did not have the same position and orientation as the exposure box.

As in Experiment 1, a  $t$  test revealed that the mean number correct for Group 1 (no panels) was not significantly different from that for Group 2 (feature panels). Nor did the two groups differ significantly in their mean number of rotational errors. Of course, the small  $n$ s mean that the between-groups comparisons have little power.

### Discussion

In Experiment 2, each rat's performance declined. On the first day, several of the rats were visibly disturbed—showing the freezing behavior that indicates fright. These observations confirmed the tentative conclusion from Experiment 1, namely, that the rats' orientation within the test box derived from their perception of the environment outside the box.

The fact that 4 rats achieved significantly more correct digs than rotational errors indicates that they used some strategy to distinguish which end of the box was which. Thus, these results show that rats can learn to use local environment to establish their orientation, when the orientation of the local environment varies with respect to the global environment. Since the rats without distinctive panels appear to have done this as readily as the rats with panels, the data suggest that the important aspect of the local environment is its shape—in this case, the shape of the tabletop. JM3, in the no-panels group, seems not to have used this strategy. With this rat, digs at the rotational equivalent of the correct location were as frequent as digs at the correct location, and both were significantly above chance. The rotationally equivalent location within the box is indistinguishable from the correct location on the basis of the shape of the box alone, but distinguishable from it if the box's relation to the tabletop is taken into account. Thus, when the shape of the room no longer sufficed to establish an orientation within the box, this rat appears to have taken its heading from the shape of the box, while 4 other rats relied on the relation between the box and the tabletop and/or the distinctive features of the panels in the corners.

Experiment 3 tested whether it was the relation between the box and the tabletop or distinctive cues within the test box that differentiated one end of the box from the other for these rats.

### EXPERIMENT 3

The 5 subjects that showed a significant tendency to dig at the correct location in Experiment 2 continued into Experiment 3, which was the same as Experiments 1 and 2, except for alterations in the experimental environment designed to force the rats to take their heading from the boxes alone, without reference to the extramaze environment. In Experiment 3, both groups of rats saw distinctive corner panels. For one group, these panels were the same as those experienced in the two previous experiments, and in the same configurations. For the other group, the panels were present only in this experiment, when the rats no longer had perceptual access to the environment outside the box.

Table 2  
Percent Digs (Out of 40 Digs) at Correct, Rotationally Equivalent, and Incorrect Locations in Experiment 2

Rats	% Correct	% Rotational Errors	% Misses	% Corner Errors
JM1 (N)	38†	10	53	30†
JM3 (N)	25*	28*	48	15
JM4 (N)	58†	15	28	0
JM5 (P)	63†	15	23	3
JM6 (P)	58†	13	30	0
Mean	48	16	36	

Note—A corner error also could have been a rotational error or a miss; therefore, the Corner Errors category does not exclude the other types of errors. N = no panels; P = panels. \* $p < .01$ , † $p < .001$ , binomial likelihood that the proportion would be this great or greater.

### Changes in the Experimental Conditions

The experimental room (2.2×2.1 m) was unlit, anechoic, and painted black. Except for the corner panels, which were added to the boxes for Group 1, the table and boxes were the same as in the preceding experiments. However, whichever box was currently in use was covered with a Masonite sheet (74×142 cm) resting on top of the feature panels, at a height of 56 cm from the table. This cover contained two symmetrically placed Plexiglas windows (each 24×66 cm) and a centered 7-W night light; it was rimmed with heavy cloth that reached below the top edge of the box (to prevent any view of the chamber and to prevent the light in the box from illuminating the room). In one corner of the completely dark room, a lidless wire cage sat on a Masonite platform (26×32 cm; 10 cm above the floor), rotating at one revolution per minute. The rats were kept on this platter during the 75-sec intratrial delay, to ensure their disorientation with respect to the room and the tabletop. Between trials, we also interchanged diagonally opposite panels, to alter the relation between the interior of the box and the tabletop. The interchange of panels was equivalent to rotating the box 180° about its own center. To detect the interchange, however, a rat would need perceptual access to a framework larger than the box, and such access was denied in this experiment. The purpose of this rotation was merely to discourage rats from relying on their sense of orientation within the room, if, despite our precautions, they retained some sense of this orientation.

### Results

When forced to rely for orientation entirely upon the box itself, no rat distinguished one end of the box from the other, despite the distinctive panels in the corners (Table 3). For each of the 5 rats, the percent digs at the correct location and at its rotational equivalent were both significantly above chance (binomial  $p < .03$ , in all 10 cases). In no case did the two percentages differ significantly from each other, by a chi-square test.

The 2 rats that had originally learned the task in the presence of feature panels showed no advantage. No rat showed a tendency to make fewer rotational errors and more correct digs over time; that is, no rat gave signs of learning to use the distinctive panels in the corners in order to discriminate one end of the box from the other.

### Discussion

The results confirm the surprising findings of Cheng (1986). When the shape of the perceptible environment

provides some basis for orientation, rats rely on this macroscopic shape, rather than on the distinctive sensory features of the surfaces that define the shape. They rely on the macroscopic shape of the perceivable environment even when it does not permit an unambiguous determination of heading, ignoring salient aspects of nearby surfaces that unambiguously define which end of the environment is which. It was both comical and poignant to see a rat munch Cocoa Puffs directly in front of, for example, the black corner panel in the exposure box and then, when placed in the test box, run to the white panel diagonally opposite the black and dig there! The rats did not use such distinguishing features as landmarks by which to orient.

The failure to take their heading from the corner panels was true both of rats never before exposed to feature panels and of rats that had received extensive training intended to help them recognize the positional fixity of the panels within a box. The small number of animals that remained in the two groups by Experiment 3 do not permit us to conclude that there was no effect of this prior experience (although the data do not suggest any). However, they do permit us to reject one hypothesis about why Cheng's rats failed to use the distinctive features of the panels in getting oriented within the box. It is clearly not because they had no experience indicating that the panels remained fixed within the box. The rats JM5 and JM8 had the requisite experience, yet they were misoriented as frequently as the 3 rats without this prior experience.

The results of Experiment 3 imply that it was the relation between the box and the tabletop that enabled 4 of the rats to distinguish the correct location from its rotational equivalent in Experiment 2. When these rats could no longer perceive this relation, they no longer distinguished between these two geometrically equivalent locations.

### GENERAL DISCUSSION

Experiments 1 and 2 confirm earlier findings (Hebb, 1938; O'Keefe & Conway, 1980; Olton & Collison, 1979; Olton & Samuelson, 1976; Suzuki, Augerinos, & Black, 1980) that rats make use of available large-scale environmental cues in navigating to a remembered location within a maze or box. In Experiment 1, the rats did not make rotational errors when run in a stable, well-lit room environment. In Experiment 2, the performance of the same rats was disturbed by the displacement and rotation of the test box within the room. Carr and Watson (1908; see also Carr, 1917) were among the first to report the dramatic effect of changing the orientation of a maze with respect to the extramaze environment, even under conditions where the extramaze environment was not perceptible to the rat once it was in the maze. Their results showed that the rat carries with it into an enclosed maze a sense of its global heading, its orientation with respect to the environment outside the maze.

Our results suggest that it is the shape of the extramaze environment that is important in establishing the rat's

Table 3

Percent Digs (Out of 30 Digs) at Correct, Rotationally Equivalent, and Incorrect Locations in Experiment 3

Rats	% Correct	% Rotational Errors	% Misses	% Corner Errors
JM1 (N)	50‡	33‡	17	7
JM3 (N)	23*	27†	50	17
JM4 (N)	33‡	30†	37	0
JM5 (P)	27†	40‡	33	0
JM6 (P)	43‡	27†	30	3
Mean	35	31	33	

Note—A corner error also could have been a rotational error or a miss; therefore, the Corner Errors category does not exclude the other types of errors. N = no previous panel experience; P = previous panel experience. \* $p < .05$ , † $p < .01$ , ‡ $p < .001$ , binomial likelihood that the proportion would be this great or greater.

heading, not other less abstract perceptual features (e.g., white-black), no matter how salient. This is consistent with the results of Ritchie (1947). He found that a 200-W light bulb overhead near the maze was a less effective extramaze cue than was a large rack of cages located some distance away.

Because of their sense of their orientation with respect to the extramaze environment, rats can have an unambiguous sense of orientation within a maze whose symmetrical shape does not by itself permit an unambiguous orientation, provided the location and orientation of the maze within some extramaze framework is constant. The default environment from which rats take their heading is the global environment (the experimental room). When, however, only a more local extramaze environment provides a stable framework, rats learn to use the relation between the maze and the more local environment (Experiment 2).

Primates show a similar dependence on the global environment in spatial tasks. Tinklepaugh (1932) arranged 8 to 16 pairs of containers upside down in a circle, permitted chimpanzees to watch as food was placed under one member of each pair, then removed the animals from the room. When returned to the room, the chimps went to the locations where food had been seen to be hidden—even when each pair of containers had been reversed so that the container at that location no longer looked like the container under which the food had been hidden. When an entire circle of containers was shifted clockwise or counterclockwise within the room, the chimps returned to the same location within the framework provided by the room, although a distinctively different container now occupied this location. Monkeys also remembered the location of hidden food more readily on the basis of room position than on the basis of the color, size, or shape of the food container under which it was hidden. Even when food was placed in one of three containers and the containers were shifted under the monkey's direct observation, the monkey chose the container in the location where he or she saw the food placed originally (Tinklepaugh, 1932).

Gallistel (in press) suggests that disoriented animals determine their position and heading within a mapped environment by computing the principal axes (or other shape parameters) of the currently perceived environment and comparing these with the corresponding shape parameters for similarly sized portions of their cognitive map. By comparing shape parameters, the animal brain computes the translation and rotation required to make the animal's position and orientation with respect to the currently perceived world congruent with a position and orientation on its cognitive map. Computing the requisite translation and rotation is equivalent to the operation of "taking a fix" in conventional navigation. If an animal computes its heading in this fashion, then the process of determining heading is a module in Fodor's (1983) sense. It must

be impenetrable to sensory data that define properties of the environment other than its macroscopic shape, no matter how relevant those properties may be to the task. The hypothesized computational process is impenetrable to perceptual properties other than shape because shape parameters, such as the principal axes, are defined by shape and shape alone.

In any event, our results and those of Cheng (1986) show that the process by which a rat determines its heading is surprisingly impenetrable by sense data that define properties of the environment other than its shape. Whether this cognitive impenetrability is complete and unalterable remains to be determined.

#### REFERENCES

- CARR, H. (1917). Maze studies with the white rat. *Journal of Animal Behavior*, 7, 259-305.
- CARR, H., & WATSON, J. B. (1908). Orientation of the white rat. *Journal of Comparative Neurology & Psychology*, 18, 27-44.
- CHENG, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition*, 23, 149-178.
- FODOR, J. A. (1983). *The modularity of mind*. Cambridge, MA: MIT Press.
- GALLISTEL, C. R. (1989). Animal cognition: The representation of space, time and number. *Annual Review of Psychology*, 40, 155-189.
- GALLISTEL, C. R. (in press). *The organization of learning*. Cambridge, MA: Bradford Books/MIT Press.
- GOULD, J. L. (1986). The locale map of honey bees: Do insects have cognitive maps? *Science*, 232, 861-863.
- HEBB, D. O. (1938). Studies of the organization of behavior: I. Behavior of the rat in field orientation. *Journal of Comparative Psychology*, 25, 333-352.
- MITTELSTAEDT, M. L., & MITTELSTAEDT, H. (1980). Homing by path integration in a mammal. *Naturwissenschaften*, 67, 566-567.
- MORRIS, R. G. M. (1981). Spatial localization does not require the presence of local cues. *Learning & Motivation*, 12, 239-260.
- O'KEEFE, J., & CONWAY, D. H. (1980). On the trail of the hippocampal engram. *Physiological Psychology*, 8, 229-238.
- OLTON, D. S., & COLLISON, C. (1979). Intramaze cues and "odor trails" fail to direct choice behavior on an elevated maze. *Animal Learning & Behavior*, 7, 221-223.
- OLTON, D. S., & SAMUELSON, R. J. (1976). Remembrance of places passed: Spatial memory in rats. *Journal of Experimental Psychology: Animal Behavior Processes*, 2, 97-116.
- POTEGAL, M. (1982). Vestibular and neostriatal contributions to spatial organization. In M. Potegal (Ed.), *Spatial abilities: Development and physiological foundations* (pp. 361-387). New York: Academic Press.
- RITCHIE, B. F. (1947). Studies in spatial learning: III. Two paths to the same location and two paths to two different locations. *Journal of Experimental Psychology*, 37, 25-38.
- SUZUKI, S., AUGERINOS, G., & BLACK, A. H. (1980). Stimulus control of spatial behavior on the eight-arm maze in rats. *Learning & Motivation*, 11, 1-18.
- TINBERGEN, N., & KRUYT, W. (1938). Über die Orientierung des Bienenwolves (*Philanthus triangulum* Fabr.). III. Die Bevorzugung bestimmter Wegmarken. *Zeitschrift für vergleichende Physiologie*, 25, 292-334.
- TINKLEPAUGH, O. L. (1932). Multiple delayed reaction with chimpanzees and monkeys. *Journal of Comparative Psychology*, 13, 207-243.
- TOLMAN, E. C. (1948). Cognitive maps in rats and men. *Psychological Review*, 55, 189-208.