A purely geometric module in the rat's spatial representation*

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Abstract

Rats were tested in place finding tasks in a rectangular environment with distinct featural panels in the corners, such as the example in Figure 1A. When given a target place to seek, they made a systematic error both in a working memory paradigm and in a reference memory paradigm: they sometimes searched at the point located at 180° rotation from the target through the centre. In a working memory paradigm, these rotational errors were almost as numerous as correct searches. The target and its rotational equivalent have the same geometric relations to the arrangement of surfaces as surfaces, or the shape of the environment, but differ in their relations to non-geometric properties such as the brightness or texture of a surface. In making systematic rotational errors, the animal must have been using some record specifying only the target's geometric relations to the shape of the environment, and not its relations to the arrangement of non-geometric information. Further tests showed that rats could use the non-geometric information, but that they primarily checked features near a geometrically specified target address, that is, an address specified by its geometric relations to the shape of the environment alone. They did not seem to use the overall arrangement of non-geometric features. It is theorized that in orienting in space by using landmarks, the rat uses primarily a purely geometric module, which also serves as a basis for coordinating the locations of non-geometric data.

Animals have diverse ways of finding their way back to desired places. Many rely on a record of some aspects of the spatial relations between surrounding landmarks and surfaces on the one hand, and the goal on the other. Such a

record, called a spatial representation here, encodes some of the spatial relations holding among surfaces and landmarks in one's physical environment, but does not necessarily dictate any particular course of action. Evidence suggests that a spatial representation is used by chimpanzees (Menzel, 1973, 1978; Tinklepaugh, 1932), nutcrackers (Balda, 1980; Balda & Turek, 1984; Kamil & Balda, 1985; Tomback, 1980; Vander Wall, 1982), marsh tits (Shettleworth & Krebs, 1982), digger wasps (Thorpe, 1950; Tinbergen, 1972), and bees (Cartwright & Collett, 1982, 1983; Collett & Cartwright, 1983; Dyer & Gould, 1983). Little is known, however, about what properties and relations among landmarks and surfaces the animals are using in navigation. This paper addresses this problem in the rat.

Recent evidence from radial maze studies has shown that the rat can keep track of a number of locations by their relations to landmarks. The radial maze has a centre platform with a number (usually eight) of long narrow arms radiating from it. Typically, it is surrounded by stable landmarks, and food is placed at the end of each arm at the start of each trial (e.g., Olton, 1978; Olton & Samuelson, 1976). If the animal is forced to traverse a number of arms to collect the bait, it will later choose to go to the unvisited arms when all the arms are accessible. Landmarks have primacy for rats in accomplishing this task. For example, suppose the animal is forced down three arms, and then trapped in an enclosure at the centre platform. If during the delay period, all the arms are rebaited, and the entire landmark array is rotated 180°, while the maze itself is not moved, the rat then behaves as if the world had rotated. It goes to places it had not been to as defined according to the rotated configuration of landmarks (Suzuki, Augerinos, & Black, 1980). Hence, the animal relies on landmarks over and above possible scent trails left on traversed arms, smell of pellets, or inertial cues, which specify positions in Newtonian space. Other studies concur in ruling out the use of scent from the food (Maki, Brokofsky, & Berg, 1979; Olton, 1978; Olton & Collison, 1979; Suzuki, Augerinos, & Black, 1980; Zoladek & Roberts, 1978), scent trails left on arms already traversed (Maki, Brokofsky, & Berg, 1979; Olton, 1978; Olton & Collison, 1979; Olton & Samuelson, 1976; Suzuki, Augerinos, & Black, 1980), and the need to rely on stereotypic motor patterns, such as going always from one arm to the one immediately on its right (Beatty & Shavalia, 1980; Maki, Brokofsky, & Berg, 1979; Olton, Collison, & Werz, 1977; Roberts, 1979, 1981; Suzuki, Augerinos, & Black, 1980). For a fuller review of these matters, see Roberts (1984).

It is not clear, however, what aspects of the landmark array the rat has encoded and used in navigation. The data here indicate that the rat relies primarily on the geometric relations between the goal and the overall shape of the environment. Non-geometric information found on surfaces, such as

brightness level, texture, and smell, are also encoded, but their use seems subordinate to the use of the shape of the environment. Experiments were run in rectangular boxes such as the one shown in Figure 1A, which has one long black wall and one long white wall, and panels in the corners distinct in visual, tactile, and olfactory characteristics. Figure 1B illustrates the geometric information contained in the environment, what has been called the shape. How surfaces as surfaces are arranged in relation to each other is shown, but not what the surfaces themselves look like. Figure 1C shows the non-geometric information found on the surfaces, also called the featural information here. Note that features also stand in geometric relations to each other. For example, the featural patterns on two panels stand at a fixed distance from each other. This will be called the arrangement of featural information, to distinguish it from the geometry in the arrangement of surfaces as surfaces, the shape of the environment. Geometric information, mentioned without qualifications, refers to the shape of the environment and the geometric relations of a goal to that shape.

The evidence for the use of geometric information comes from systematic errors that the rat makes in place finding tasks. Within a rectangular environment, rats confuse geometrically equivalent locations, locations that stand in the same geometric relations to the shape of the environment. Suppose that the filled dot in Figure 1A is the location sought. Because of the rotational symmetry in the environment, one other location stands in the same geometric relations to the shape of the environment as the target. The rotational equivalent (the open circle) is located at 180° rotation from the target through the centre of the environment. To see this, imagine a record specifying only the shape of the environment plus the location of the target within that shape, such as Figure 1B, with the dot representing the target. This record can be matched to the actual environment in two equally good ways, one 'correct' congruence, and one 'erroneous' one that arises when the record is rotated 180° with respect to the environment, with the top wall in Figure 1B lining up with the bottom wall in Figure 1A. The latter match is a match solely on geometric grounds. If the target were specified by its relations to the arrangement of featural information, for example, as in Figure 1C, only one match between map and environment can be found. Here, when the map is rotated 180° with respect to the environment, the non-geometric information on the map would not match the non-geometric information in the environment, even though the surfaces on the map line up with the surfaces of the environment. The two geometrically correct locations are distinguishable by their relations to the arrangement of features. For example, of the two, only the target is near a white wall. Systematic rotational errors, searching at the geometrically correct location that is featurally wrong, means that on

a systematic proportion of trials, an animal has got the geometric relations between the target and the shape of the environment right, and only that. Thus, it must have encoded and used geometric information.

A second research strategy, transformation tests, was also used to assess the relative importance of geometric and featural information in defining a

Figure 1.   *Geometric and featural information in the rectangular box used in Experiment 1B. A. A plan view of the environment. Three walls are black while one is white. Panels differing in visual, tactile, and olfactory characteristics are in the corners. The filled circle represents the location of hidden food. B. The shape of the environment, which contains geometric information. Specifying the target's location only by its geometric relations to the shape results in an ambiguous specification of the location. The open circle in the lower left in (A) stands in the same geometric relations to the shape of the environment as the correct location, and cannot be distinguished from the correct location on geometric grounds alone. C. The arrangement of featural information, with the letters W and B representing white and black. Specifying the target's relation to this information provides an unambiguous specification of the place. For further explanation, see text.*
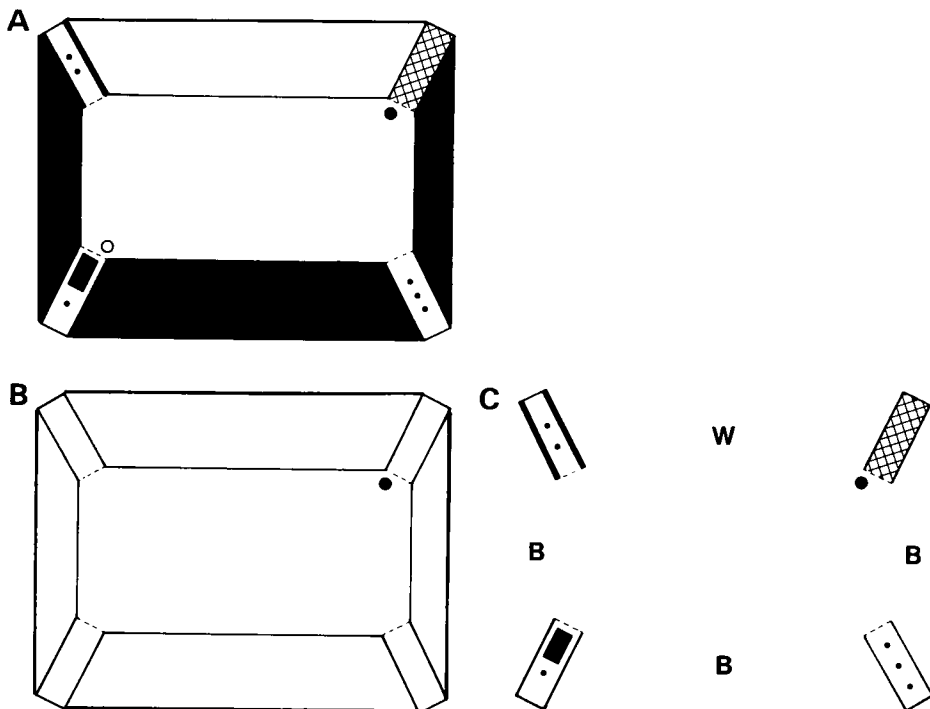
place. Here, the animal first learns over trials to find a target location. Then spatial properties about the target location are changed. Changing the properties that are crucial in specifying a place ought to lead to declines in performance. Contrasts were made between transformations that altered the geometric relations between the target and the shape of the environment, and those that preserved those geometric relations, but altered the arrangement of featural information. The nature of the transformations is explained in the experiments that follow.

Experiment 1: Working memory tasks in a rectangular box

In this experiment, rats were tested in working memory paradigms in a rectangular field surrounded by walls (Figures 1 and 2). The target location was chosen at random on each trial. A rat was shown the food, allowed to eat some, and then removed. A short time later, it was to relocate the food, now buried at the same location.

Apparatus

The rectangular environment was a wooden box (120 × 60 cm) filled with 9 cm of pine chips (Pine-dri bedding). The semi-glossy black walls enclosing the box (38 cm tall) were separable from the bottom. Multimodally distinct panels, 11 cm wide by 33 cm high, cut off the corners at an angle of 30° with the long wall and 60 with the short wall. One panel was made of dark masonite of a smooth texture, had one dim point of light shining out of it, one stripe in the middle, and a hole just above ground level behind which was a wad of cotton with a drop of anise on it. One was made of light masonite of a smooth texture, had two dim points of lights shining out of it, and a stripe down each side, with no odour cue. One was made of unpainted light masonite of a rough texture, had no points of light shining out of it, and a hole just above ground level behind which was a wad of cotton with a drop of peppermint on it. A fourth panel was made of shiny sheet metal, with three points of light shining out of it, and no odour cue. The odours were clearly discernible to a human nose even at the end of a session. In Experiment 1B, a white styrene sheet was inserted along one entire long wall to provide additional salient featural information. A rat's eye view of this apparatus appears in Figure 2. A 7-watt light 62 cm above the middle of the box provided the only lighting in the sound-proof experimental chamber (2.1 × 2.2 m and painted black).

Figure 2.   *Photographs of the two ends of the experimental enclosure used in Experiment 1B, taken from the rat's perspective at the centre of the enclosure.*
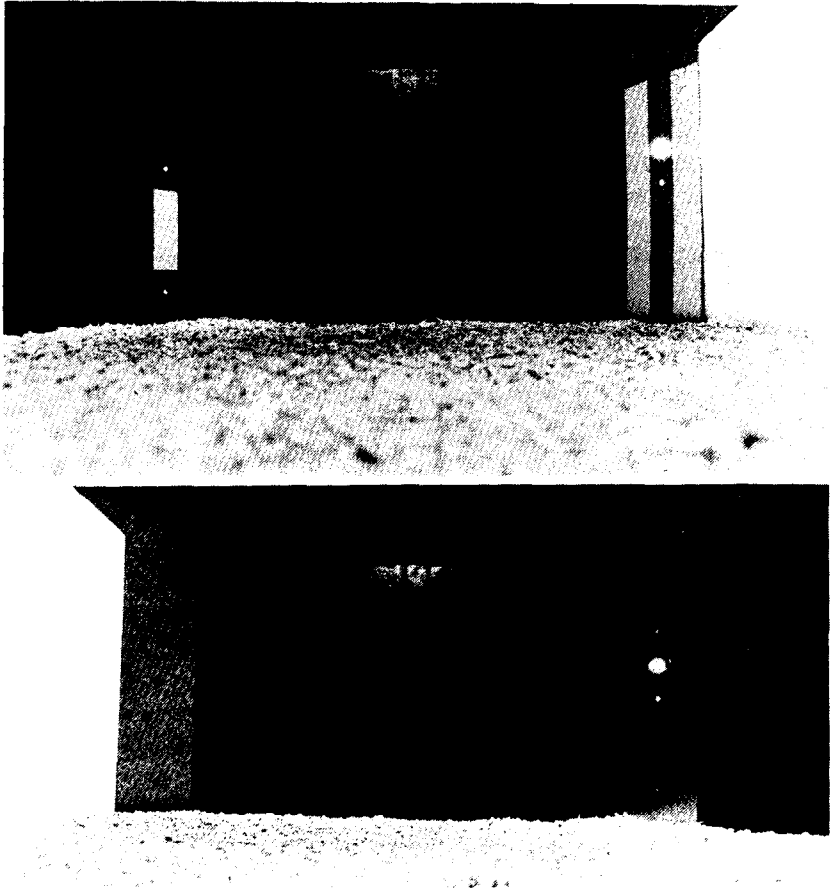
Experiment 1A

Method

Subjects

Three male Sprague-Dawley rats, aged 157 days at the start of the experiment, served as subjects. Experimentation started about four hours into the dark cycle, with the animals deprived of food for about four hours.

Apparatus

Two identically constructed replicas of the experimental set-up were made. The rats were exposed to food in one box, called the exposure box, and tested for recall in the other, the test box. This minimized the delay period and eliminated the use of scent that an animal might leave behind to mark the location of food. The items that made up each environment were regularly cleaned and identical components were randomly interchanged from day to day.

The bottom of each box was divided by nine grid lines parallel to each wall into 100 12 × 6 cm rectangles. The wooden food dish (12 × 6 × 1 cm) always rested on the bottom with its centre on one of the intersections of the grid, the long side of the dish parallelling the long walls.

Procedure

The animals were first familiarized with the apparatus by being placed in the box for an hour a day over three days. Some food used as reward, the commercial cereal Coco Puffs, was available. The rats were then given nine training trials (one per day) where the food was only partially buried on the recall test. Nine different reward sites in the box, excepting the centre, were chosen for each animal. On any two successive days, these locations were not adjacent. Procedurally, the boxes were moved to a random location within the experimental chamber. The bedding in each was thoroughly shuffled. Seven pellets of Coco Puffs were placed in the food dish in the exposure box, four in the dish in the test box. The bedding was then brushed uniformly flat in both boxes. A pit was dug out over each food dish, leaving the dishes barely covered by bedding. The rat was placed in the exposure box to find and eat some cereal. If it had not eaten any food in two minutes, the dish was completely exposed. If it still had not eaten in another two minutes, it was placed at the food. If it still had not eaten after another three minutes, it was removed. An animal that ate was removed when it bit into the third pellet. The rat was then placed in a cage outside the chamber for the 75 s delay period (plus or minus 5 s because the animals were handled in the dark). The experimental environments were moved randomly in the chamber. When put in the test box, the rat was given two minutes to find the 'remaining' four pellets. After that, the food was completely exposed. If it still had not eaten in another two minutes, it was placed at the food. If it still had not eaten in another three minutes, it was removed. An animal that ate was allowed to finish all the food. On every occasion in which a rat was placed in a box, it was placed at one of eight locations at random. These were

the middle of each of the four walls, facing the centre, or at the centre of the box, facing the middle of one of the four walls.

The rats were then tested for two trials a day, six days per week for seven weeks. The trials in a day were separated by 1.5 to 2 hours intertrial time to minimize any proactive interference from the first trial on the second. The 12 reward sites for each week were randomly chosen for each rat, subject to these constraints: A location was used at most once a week. On any two successive trials, locations of food were not adjacent. Three locations were chosen from each quadrant. The locations on the centre lines of the grid were arbitrarily assigned to quadrants. The centre was not used.

The procedure was similar to that during training. The environments were set up in the same way except for the bedding over the food dishes. The bedding was uniformly flat in the test box, with the food buried under the bedding. In the exposure box, the food was completely buried in the first three weeks, while it was barely covered with bedding (as in the training phase) in the last four weeks. The food in the exposure box was at first buried to see if the rats could find it by cues emanating from it alone. They had no systematic success. The food was then partially exposed in the exposure box in order to reduce digging at wrong locations, minimizing proactive interference arising from the activity of digging at locations where food was not found. On each trial, the rat was first placed in the exposure box and allowed two minutes to find and eat the food. After that, the animal was given two more minutes with the food partly exposed during the first three weeks when food was buried, and removed during the last four weeks when food was partly exposed. In the former case, a sizeable pit was dug out over the dish so that the food was barely covered. A rat that ate was removed after it bit into the third pellet. During the delay period of 75 (plus or minus 5) seconds, the boxes were moved randomly within the experimental chamber. The animal was then placed in the test box. If it had not found the food in two minutes, a sizeable pit was dug over the food dish. If the animal had not eaten in another two minutes, it was removed. On each occasion in which a rat was placed in a box, one of the eight locations used in the training phase was again chosen at random.

Dependent measure

To count as a dig, the rat had to scratch out bedding at a localized area, and at least stick its nose to the ground. Merely scratching the surface, sticking its nose just under the surface, or running around with the head just under the surface did not count. Most of the time, a dig involved concerted effort and was unambiguous. The location of the dig (the centre of the deepest part

dug out) was recorded to the nearest half unit on both axes according to the grid on the bottom of the box.

Results

On the majority of trials, the rats either dug at the correct location or made a rotational error, digging at the location 180° rotation from the correct location through the centre. They dug about equally often at these two locations. Other errors were nonsystematic. The data from the last five weeks of testing were analyzed for individual animals. All p values refer to chi square tests.

The locations at which the rats first dug were classified into one of three categories. If a dig was within 15 cm of the centre of the food dish, it was correct. If it was within 15 cm of the location at 180° rotation through the centre from the food dish, it was a rotational error. Other errors were called misses (Table 1). The rats chose the correct location and the rotational error systematically. A circle of 15 cm radius covers 10% of the surface area. The proportion of correct digs and rotational error both far exceeded this figure in each rat ($p < .001$ in each case). In contrast, between correct digs and rotational errors, a chance expectation of a 1:1 ratio cannot be rejected in any of the animals ($p > .10$ in each).

A number of variables did not affect the distribution of correct digs, rotational errors, and misses in any animal: first trial *vs.* second trial in a day, the extent to which the environment was translated in the room, the quadrant in the box where the food was, whether the food was by the periphery or not, whether the food was near a corner or not. One variable that had an effect on one and only one animal was the extent to which the box was rotated during the delay period. The proportion of rotational errors to correct digs increased with the degree to which the test box was rotated with respect to the exposure box ($p < .01$). This phenomenon is discussed in the next experiment, where it occurs with more force.

The use of cues emanating from the food was highly unlikely. When the animals were put in the exposure box with the food buried, they had no systematic success at locating it. They also dug systematically at locations not containing food.

Discussion

In sum, the rats systematically made rotational errors, almost as many as correct digs. This shows that they had been relying on the geometric relations

between the goal and the shape of the environment. These mistakes are correct in that regard, but wrong in terms of the relations between the goal and featural information. The extent of rotational errors shows that the animals relied little on the arrangement of features to disambiguate geometrically equivalent locations. To cast this quantitatively, suppose that only a shape record like Figure 1B is used. The correct location and the rotational error are then both best fits between record and environment, depending on which of two ways the rectangular shape specified by the record is matched with the rectangular environment. Use of a shape record alone on every trial should give 50% correct digs and 50% rotational errors. The rats' performance approached this ideal but deviated in two respects. They missed 22% of the time, and they also searched slightly more often at the correct location. The 3:2 ratio of correct digs to rotational errors means, however, that the animals were only 20% above chance at distinguishing the correct location from the rotational error. One interpretation then is that 78% of the time, the rats used a shape record and found a geometrically correct location, but only 20% of the time did they use some record of featural arrangement to disambiguate the two geometrically correct locations. Performance is dominated by the use of some record specifying only the shape of the environment.

Table 1.   *The percentage of trials on which individual rats in Experiments 1A and 1B dug at the correct location, made a rotational error, or dug elsewhere or not at all (Misses). The correct location varied randomly from trial to trial*

Experiment 1A: Environment with four panels and all walls black.

Rat	Correct digs	Rotational errors	Misses
An	47	33	20
De	55	35	10
Th	38	25	37
Average	47	31	22

Experiment 1B: Environment with four panels, one long wall white and one long wall black.

Rat	Correct digs	Rotational errors	Misses
An	46	26	29
De	42	25	33
Th	46	22	32
Average	44	25	31

Experiment 1B

This experiment is a continuation of Experiment 1A with more blatant featural information added to the environment. One entire long wall of the box was rendered white. Hence, both long walls as well as the corners provided distinctive featural information that could serve to disambiguate geometrically equivalent locations.

Method

Subjects

The same subjects continued in this experiment. They were 276 days old at the start of the experiment. Between the two experiments, they were trained for 108 more trials under the procedure used in the last four weeks of Experiment 1A, with various combinations of stimuli in the corners. This experiment started each day around the start of the animals' dark cycle, after they were deprived of food for 13 to 15 hours.

Apparatus

Except for one modification, the apparatus was the same as Experiment 1A's. A white styrene sheet was inserted to cover an entire long wall, though not the panels in the corners. It was always on the same side with respect to the panels in the corners.

Procedure

Except for one change, the procedure used in the last four weeks of testing in Experiment 1A was used. The only difference concerned the extent to which the environment was rotated during the delay period: in a week, each animal had the same number of small ($<60°$), medium ($60°$ to $120°$), and large ($>120°$) rotations. The rats ran two trials a day, six days a week, for six weeks. Again, only data from individual animals were analyzed, and p values refer to chi square tests.

Results

The results (Table 1) resemble those of Experiment 1A. With the same scoring criteria as Experiment 1A, the rats, on most trials, either dug at the

correct location or made a rotational error. They each dug slightly but not significantly more often at the correct location. Both the proportion of correct digs and the proportion of rotational errors far exceeded the chance figure of 10% ($p < .001$ in each rat). No other systematic errors were found.

Discussion

Calculating the figures in the same way as Experiment 1A, on 69% of the trials, the rats dug at a geometrically correct location. Correct digs exceeded rotational errors by 28%, and for each animal, this proportion was not statistically higher than the equivalent figure in the previous experiment. Despite the increased salience of the featural information, the rats continued to rely primarily on the geometric relations between the goal and the shape of the environment. Likely, the 20% and 28% estimates for the use of featural information to disambiguate geometrically equivalent locations reflect above chance figures that the statistics are not sensitive enough to show. Each rat in both experiments made more correct digs than rotational errors. If they did use featural information, however, the extent is clearly far less than the use of some record specifying the geometric relations between the target and the shape of the environment.

Considering the effects of the same variables examined in Experiment 1A, again, all but the degree through which the environment was rotated in the delay period had no significant effect on the outcome in any rat. Two rats were more likely to commit a rotational error the more the environment was rotated in the delay period ($p < .01$ in each), though the proportion of geometrically correct digs did not differ according to the extent of rotation in the delay period. This means that the geometrically correct location that these rats chose on a recall test tended to lie in roughly the same compass direction from the centre of the box as the location they were shown when exposed to the food before the delay. The rats were not likely using extramaze cues here, since the extent to which the box was translated in the room in the delay period, something that drastically affects the geometric relations between the experimental apparatus and the room, had no effect. They were probably keeping track of compass direction by inertial means, chiefly using their vestibular sense. Potegal (1982) and O'Keefe & Conway (1980) with rats, Mittelstaedt & Mittelstaedt (1980) with gerbils, and Etienne (1980) and Etienne, Teroni, Maurer, Portenier, & Saucy (1985) with hamsters, have found rodents to be capable of keeping track of the degree of rotation when they were passively moved. If the interpretation is correct, rats here used inertial information over and above featural information, de-

spite the fact that the reward contingencies cried out for the use of featural information. This phenomenon indicates that the topic of inertial navigation deserves far more study.

In conclusion, however, the retention and use of both featural and inertial information are subsidiary to the use of the geometric relations between the target and the shape of the environment. The rats chose mostly geometrically correct locations, regardless of how the box, with its featural properties, was rotated in the delay period.

Experiment 2: Reference memory tasks in a rectangular box

Experiments 2 and 3 explored how rats use featural information in specifying a place. Experiment 2 attempted to verify that rats can use the featural information in the experimental box under some circumstances. Experiment 1 left this point unclear. Rats were run in both versions of the apparatus used in Experiment 1, with and without the white wall. For each rat, the food was always at the same corner of the box from trial to trial. The animals learned to choose the correct corner more often than its geometrically equivalent diagonal opposite in both versions of the box. A manipulation then tested whether featural information near the target location was crucial for disambiguating geometrically equivalent locations. In the box with all walls black, the panels at the correct corner and at its diagonally opposite corner were removed. This made the featural information identical at the target and its diagonal opposite. Featural information distant from the target must be used to distinguish it from its diagonal opposite. If featural information close to the target is crucial for disambiguating geometrically indistinguishable locations, performance should decline, but decline in a particular fashion. As the target can still be distinguished from its adjacent corners by their different geometric relations to the shape of the environment, the animal should not commit more errors at adjacent corners. The increase in errors should come solely from making rotational errors at the corner diagonally opposite the target.

Method

Subjects

Four experienced male Sprague-Dawley rats, aged 123 days at the start of the experiment, served as subjects. They had seen a four-arm radial maze

environment, but had not seen the apparatus used here prior to this experiment. Experimentation started around the start of the animals' dark cycle, after they had been deprived of food for 13 to 15 hours.

Apparatus

The apparatus was identical to the one used in Experiment 1. Both versions of the box, with and without the white wall, were used.

Procedure

The task confronting the animals was to choose the one corner out of four where food was available. Each panel was assigned to one rat as the correct corner. On a trial, a cylindrical glass bottle (7.8 cm tall, 4.2 cm in diameter) full of Coco Puffs stood upside down in each corner, at the middle of the panel. If the animal knocked over the bottle in the correct corner, food spilled out. Bottles at incorrect corners were fitted with invisible caps that prevented food from coming out. The rat was allowed to knock over bottles until it found the right one.

The conditions under which the animals were tested are summarized in Figure 3. Each animal ran 10 trials per day. The experiment started with the set-up used in Experiment 1B, in which one long wall was white while the other was black (Figure 3A). Only one arrangement of one of the two sets of apparatus was used in this phase.

Each rat was first shown which corner was correct by a number of forced-correct trials on which only one bottle was in the box, in the correct corner. The animal was given four minutes to knock over the bottle and spill the food. After that, the bottle was knocked over for it. If the rat had not eaten in another minute, it was removed. A rat that started eating was removed after it bit into the second pellet. Forced-correct trials continued until an animal had bitten into a pellet within a minute of being placed in the box on five consecutive trials. After that, testing began immediately. The only difference on a test trial was that bottles were at all the corners, allowing for the possibility of errors.

A rat was trained until the day it both made a streak of nine correct responses in 10 consecutive trials (counting possibly trials from the previous day) and maintained at least a 60% performance level over the last three days. (A rat making a 9/10 streak in under three days was passed on to the next phase.) It was then tested in a rotational transfer (Figure 3B). A new set of identical stimuli was set up in the same way for this transfer test. New walls, panels, and white sheet were used. The panels and white sheet could

be fitted in two ways on the walls, the ways differing only by a rotation. Both of these otherwise identical arrangements were used, five times each in a day, ordered randomly. Rotating the stimuli at random controlled for the possible use of odours left on the substrate or on the walls of the box. To control for cues from the food, all the bottles now had caps on them preventing food from coming out. If the animal knocked over the correct bottle, however, a number of pellets of Coco Puffs were poured on the ground at the corner of the fallen bottle. The procedure was otherwise the same as before. An animal was given up to 20 trials to make a 9/10 streak. If it failed to make the criterion, it was retrained in the conditions of the first test phase until the criteria used there were again met.

In the next test phase, the environment used in Experiment 1A was used (Figure 3C). This had only the four panels in the corners, with the rest of the walls black. Only one set of stimuli in one arrangement was used. Testing began after five forced-correct trials. The procedures and learning criteria of the first test phase were used.

In the last test phase, the panels at the correct corner and at the corner diagonally opposite to the correct corner were removed (Figure 3D). After five forced-correct trials, each rat was run for 120 trials.

On any trial, the bedding in the box was thoroughly shuffled and brushed even beforehand. The entire environment was rotated at random to a different orientation within the experimental chamber. Eight possible orientations 45° apart were used. The animal was placed in the middle of the box, facing at random the middle of one of the four walls, subject to the constraint that it faced the same wall (defined with respect to the panels) at most two trials in a row.

Results

All the rats learned to go first primarily to the site with food in the first environment, with the white wall. No animal suffered a significant drop in performance in the rotational transfer test. All four rats also learned to choose the correct corner first in the environment without the white wall, but with all four panels. On the whole, the rats made more diagonal errors (rotational errors) than expected from an even distribution of errors. In the last test phase, where the local featural information (panels) at the correct corner and its diagonal opposite was removed, the rats' first choices consisted almost exclusively of either the correct corner or the diagonal error, in about equal numbers. The data were again analyzed in individual animals only. Unless otherwise mentioned, chi square tests were used.

Figure 3.   *The set-up and results of Experiment 2. A. An environment with one white wall and three black walls, and featural panels in the corners. B. A rotational transfer test in which all the features might be rotated 180° from trial to trial. C. An environment with four black walls, with featural panels in the corners. D. An environment with four black walls, and only two featural panels. The panels at the corner with food and at the corner diagonally opposite to that had been removed. The results show the percentage of trials the animals as a group chose, at asymptote in each set-up, the correct location (filled circle), the corner adjacent to the correct corner along the short wall, the corner diagonally opposite the correct corner, and the corner adjacent to the correct corner along the long wall. Different rats had different target locations. The results from the rotational transfer phase have been included in panel A.*
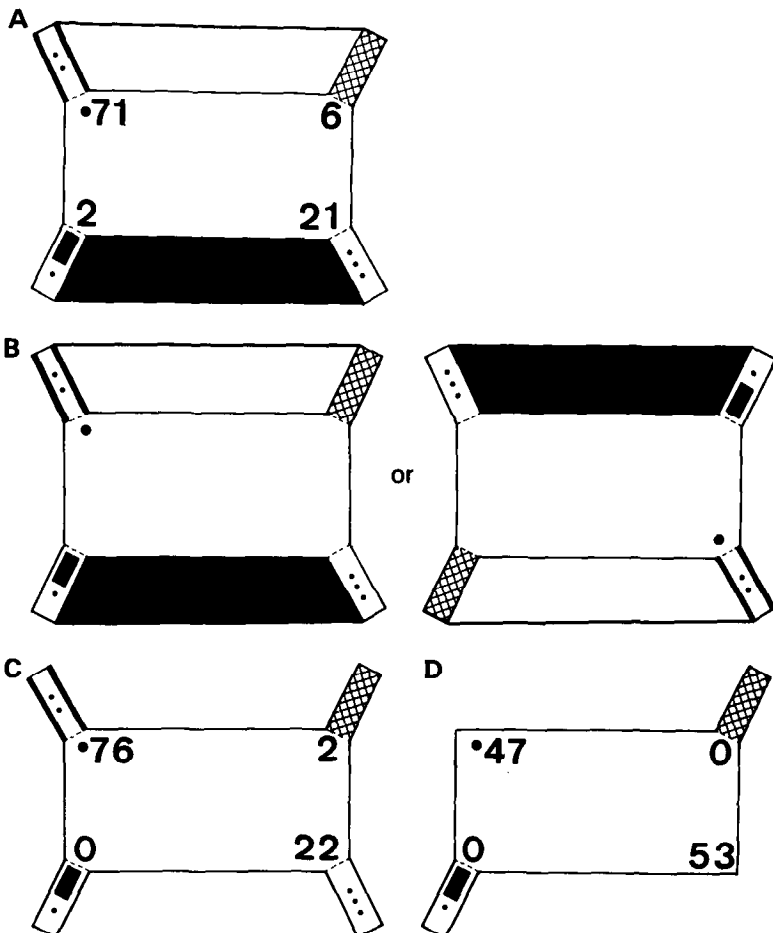
Group data on the corner of first choice at asymptote in the first environment (Figure 3A) include the last 30 trials in the first test phase in the environment with the white wall, the rotational transfer phase, and any retest trials in the original environment. Compared to asymptotic training performance, no rat chose the correct corner less often in the rotation phase, although two just missed criterion in the rotation phase. In the first test phase, the rats started their criterial 9/10 streaks on trials 9, 22, 26, and 79. In Figure 3A, each rat chose a corner with the correct geometric properties (the diagonal error or the correct location) more often than a geometrically incorrect corner ($p < .001$ in each). Each also chose the correct corner more often than its diagonal opposite ($p < .05$ in one; $p < .01$ in one; $p < .001$ in two).

The error pattern for each rat in Figure 3A was nonrandom. Three were more likely to make the diagonal error than the other errors: diagonal errors exceeded 1/3 of all errors ($p < .01$ in one; $p < .001$ in two). The fourth rat's errors differed significantly from an even distribution ($p < .05$) by concentrating at the diagonally opposite corner and at the corner adjacent to the correct corner along the long wall.

When the rats were tested in the environment without the white wall, but with all four panels, they started their criterial 9/10 streaks on trials 4, 16, 27, and 109. In their last 30 trials (Figure 3C), each rat chose the correct diagonal more often than the incorrect diagonal ($p < .001$ in each case). Three rats chose the correct corner more often than the diagonal error ($p < .01$ in one; $p < .05$ in two). One, largely because of a day of poor performance, did not. But counting its last 40 trials, it did choose the correct corner more often than its diagonal opposite ($p < .05$). Thus, all the rats learned to choose the correct corner in preference to the diagonal error.

The errors made in this environment were dominated by diagonal errors. With too few incorrect trials to use the chi square test, binomial tests (one-tailed) were run on individual error patterns. For all rats, significantly more than 1/3 of the errors at asymptote were diagonal errors ($p < .05$ in one; $p < .01$ in two; $p < .001$ in one). Combining the rats' asymptotic performances in the two environments, 81% of all errors were diagonal errors.

In the last phase, where the panels at the correct corner and its diagonal opposite were removed, all rats chose one of those two locations first on practically all trials, but chose each equally often. Errors thus consist almost exclusively of diagonal errors ($p < .001$ in each rat). Performance showed no tendency to improve over time. In the last 50 trials (Figure 3D), each rat was above chance in choosing the correct diagonal ($p < .001$ in each case), but none chose the correct location significantly more often than the diagonal error.

Discussion

Three points can be made from this experiment. First, the featural information in the box is discriminable to rats, and used under some circumstances to direct the search for food. The correct corner and its diagonal opposite stand in the same geometric relations to the shape of the box. To distinguish the two, which the rats did in both versions of the box, featural information must be used.

Second, diagonal errors were systematic. This suggests that the rats were still sometimes relying only on the shape of the box in seeking the target. To cast this quantitatively, consider Figures 3A and 3C together. Combining the results, 95% of the trials at asymptote were geometrically correct. The rats were 90% above chance. Considering the geometrically correct trials only, the rats on average chose the correct corner 77% of the time and the diagonal error 23% of the time. They were 55% above chance. This proportion is significantly lower than the proportion of geometrically correct trials by an ANOVA test on these figures for individual performances in the two environments ($F (1,9) = 35.20, p < .001$). The rats had an easier time choosing a geometrically correct corner, which can be done by using only the geometric relations between the target and the shape of the box, than choosing between two geometrically correct corners, which required the use of featural information.

Third, in distinguishing geometrically equivalent locations, the rats seemed to require featural information at the geometrically correct corners. When this was removed in the last test phase, they failed to use the remaining featural information at the corners distant from the target to distinguish the correct corner from its diagonal opposite. The failure here also shows that odours emanating from the food, the walls, the panels, or the substrate were not used. As the arrangement of stimuli was constant from trial to trial, all these possible sources of information continued to be available. The rats continued, however, to rely on the relation between the target and the shape of the environment, as they chose only geometrically correct corners. The systematic diagonal errors throughout this experiment suggest that rats sometimes rely on a mental unit encoding only the shape of the environment. This is elaborated further in the General Discussion.

Experiment 3: Transposition, affine transformation, and reflection in a rectangular box

This experiment uses the transformational strategy to further assess how important geometric relations between the target and the shape of the environ-

ment are when rats use featural information. Rats were retrained to go to one corner for food in the rectangular box without the white wall used in Experiment 1A (Figure 4A). After they had learned, two kinds of transformations preserving local featural information (the panel by which food was found) followed. One kind changed the geometric relations between the goal and the shape of the environment, while one did not.

The first transformation, the diagonal transposition, was made by switching the locations of one and only one pair of diagonally opposite panels with each other (Figure 4B). This alters many geometric relations in the arrangement of features, but preserves all geometric relations between the target and the shape of the environment. It alters both the angles and distances between panels (metric properties) and which panel is to the left or right of which (known as sense in geometry). If a rat relied on these geometric properties in the arrangement of featural information, its performance should be perturbed. The diagonal transposition, however, does not change the geometric properties of the food's location within the shape of the environment, nor does it change the featural information near the target location. If the rat relies on the shape of the environment plus the featural information near the target location, its performance should not be perturbed, despite the fact that the overall arrangement of featural information after the transformation cannot be matched up with the arrangement before the transformation.

The next transformation was either an affine transformation or a reflection. In earlier work (Cheng & Gallistel, 1984), where a fuller account of geometric considerations was given, both transformations led to decrements in performance. In the affine transformation, each panel is moved one corner over, all in a clockwise or counterclockwise direction. In a reflection, neighbouring pairs of panels along either the long walls or the short walls exchange places. In both cases, the food stays under the same panel as before. These transformations each change the featural arrangement less drastically than the transposition. The transposition is arrived at by combining a reflection and an affine transformation. Hence, it changes both the geometric properties in the arrangement of features altered by the affine transformation and those altered by the reflection. The affine transformation and the reflection both, however, alter geometric relations between the target and the shape of the environment. The food always ends up in a geometrically different corner from before. If it was at a corner where the long wall was to the right of the short wall before, it would be at a corner where the long wall was to the left of the short wall after, and vice versa. If the geometric relations between target and shape of environment are important, the rats ought to suffer decrements in performance upon encountering these transformations.

Method

Subjects

The rats from Experiment 2 continued as subjects. They were 152 days old at the start of the experiment.

Apparatus

The apparatus used was the same as in Experiment 1A. Only one replica of the environment was used.

Procedure

The three phases of the experiment involved different arrangements of panels, but all followed the procedures of Experiment 2. In the first phase (Figure 4A), the animals were retrained in the set up they faced in Experiment 2 before two of the panels were removed. That is, all the walls were black, all the panels were arranged as before, and the food was where each rat had found it before. Five forced-correct trials preceded this phase. The animals were run for 10 trials a day for four days. If they were more than 75% correct on the last three days, they were moved on to the next phase. Otherwise, they were run for up to two more days. If they had not reached criterion by then, they were dropped.

In the next phase, a diagonal transposition was effected on the environment for each rat by interchanging the panels at the location of food and its diagonal opposite (Figure 4B). The food remained under the same panel as before. Rats were tested in this condition for four days, 10 trials each day.

In the next phase, either an affine transformation (for one rat) or a reflection (for two rats) was effected on the set-up for that rat in the previous phase (Figure 4C). In an affine transformation, each panel was moved one corner over, all in a clockwise or counterclockwise direction. In a reflection, neighbouring panels along the long walls or the short walls exchanged places. The food remained under the same panel as before in both cases. Rats were tested for four days, 10 trials each day. In discussing results, the statistical test used is again the chi square test unless otherwise indicated.

Results

Three of the animals relearned the task in the retraining phase. One failed to reach criterion and was dropped. It chose the correct corner 57% of the

Figure 4.   *The phases of Experiment 3, along with the results. A. The retraining set-up. B. A diagonal transposition of the retraining set-up. C. An affine transformation or reflection of (B). Only a reflection is shown, but the affine transformation was used for some rats. The results are averaged across the three out of four animals that made criterion in retraining. They show the percentage of trials the animals chose the correct corner (filled circle), the corner adjacent to the correct corner along the short wall, the corner diagonally opposite the correct corner, and the corner adjacent to the correct corner along the long wall. Different rats had different target panels. Asymptotic data in the retraining phase (last 30 trials), and the entire transposition and affine or reflection phases are included.*
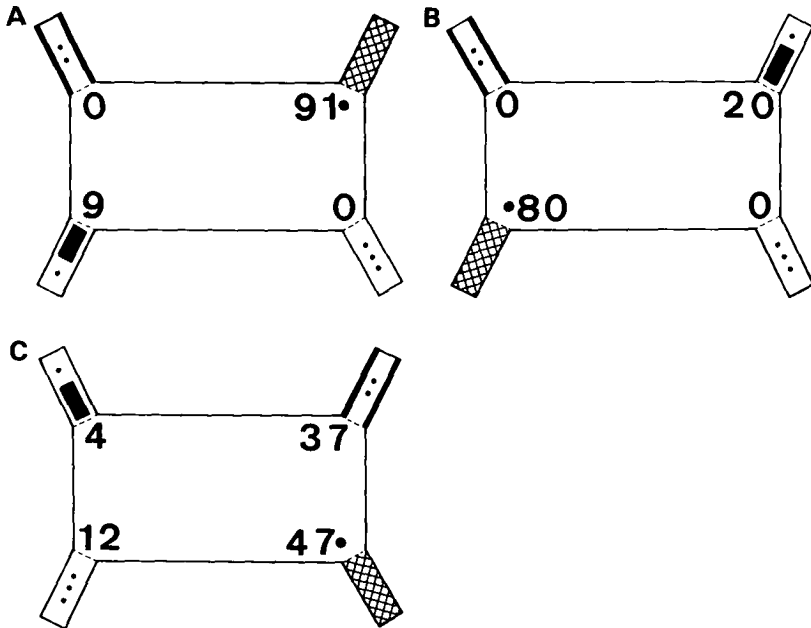
time in its last 30 retraining trials, and the diagonal error 43% of the time. It chose a corner with the correct geometric properties, but did not use featural information to disambiguate the two geometrically correct locations. At asymptote, all rats were above chance at choosing the diagonal with the correct geometric properties ($p < .001$ in each). The three rats that made criterion also chose the correct location more often than the diagonal error (Figure 4A; $p < .05$ in one; $p < .001$ in two). When the diagonal transposition was made, none of the three animals' performance (proportion of correct choices) dropped significantly (Figure 4B). When either the affine

transformation or reflection was then made, however, each showed a significant drop in performance (Figure 4C; $p < .05$ in one by the Fisher exact test; $p < .01$ in another; $p < .001$ in the third).

The error patterns in this experiment show a similar pattern to Experiment 2 in the retraining and transposition phases; they were exclusively diagonal errors. But the errors show a different pattern when the affine transformation or reflection was made; they were scattered, with one rat actually making more non-diagonal errors than expected ($p < .001$). Each rat made proportionally more diagonal errors in the retraining and transposition phases combined than in the reflection or affine transformation phase ($p < .001$ in one; $p < .01$ in two by the Fisher exact test). Thus, in this last phase, when the geometric relations between the target and the shape of the environment changed, the rats showed a lingering tendency to stick to the diagonal that previously had the correct geometric properties.

Discussion

The animals suffered no decrement in performance on encountering a diagonal transposition, while performance declined in every case when an affine transformation or reflection was made. The rats had not been simply heading for a featural pattern (panel) regardless of its geometric context, since a change in its geometric relations to the shape of the box, by an affine transformation or reflection, resulted in decrements. The decline can be attributed to changed geometric relations between target and shape of environment, and not to changes in the arrangement of featural information. A more drastic change in the arrangement of features than either the affine transformation or the reflection, the diagonal transposition, resulted in no decrements.

In specifying a place, rats seem to rely on its geometric relations to the shape of the environment, plus features near the geometrically specified target place. That features at a geometrically specified location are used suggests an organization of featural information dependent upon some shape or geometric record of the environment. The notion is elaborated further in the General Discussion.

General discussion

The results show the following points: (1) In a place finding task within a rectangular box, rats made systematic rotational errors in both working mem-

ory (Experiment 1) and reference memory (Experiment 2) paradigms. In the working memory paradigm, rotational errors were almost as numerous as correct choices. This shows that the rats must have encoded and used the geometric relations between the target and the shape of the environment. These errors are at locations correct in that regard, but incorrect in their relations to the arrangement of features. The rats, on a systematic proportion of trials, got only the geometric information right. (2) In reference memory paradigms, rats chose the correct location more often than its geometrically equivalent opposite (Experiment 2), indicating that they were also using featural information in choosing a place. (3) When featural information at the target corner and its diagonal opposite was removed, performance declined, but in a particular fashion (Experiment 2). The animals continued to choose a geometrically correct corner (the correct corner or its diagonal opposite), but did not use featural information distant from the target to distinguish between the two geometrically correct corners. (4) When the geometric relations between a target and the shape of the environment were changed, as in the affine transformation or reflection (Experiment 3), previously successful performance declined, whereas the overall arrangement of featural information could be altered substantially, as in the diagonal transposition, without adversely affecting performance.

The systematic errors that the rat makes, the rotational errors, indicate the kind of geometric relations used to specify places. To systematically confuse only the rotational error, and no other location, with the correct location, the rat must have recorded the metric relations of distances and angles between target and shape, and kept track of left–right relations, or sense. Metric relations and sense together are known as displacement properties, the set of properties staying constant when an object or cluster of objects is rigidly displaced in space. If the geometric specification did not include both metric properties and sense, other systematic errors should appear, and the rat makes no other systematic errors.

To see this, refer again to the shape record shown in Figure 1B. Suppose that sense is not kept track of. This amounts to recording the distance of the target to a long wall and to a short wall, but not whether the nearest long wall is to the right or left of the nearest short wall. The figure can in effect be reflected. Not only is a rotational error a match between record and environment, but the two corners adjacent to the correct corner as well. The animal should make systematic reflection errors at quadrants adjacent to the correct one. Similarly, suppose that metric relations are not kept track of, for instance, that the record may be uniformly squashed or stretched along its principal axes to any extent. Such a specification preserves affine properties, or all geometric properties except distances and angles. In this case, with

a squash of the length by half and a stretch of the width by a factor of two, matches at the two quadrants adjacent to the correct one can again be found. That rats do not systematically make affine or reflection errors at quadrants adjacent to the correct one, but do make rotational errors, indicates that they encode and use both metric relations and sense, or the displacement properties, between target and shape of environment.

A geometric module

The way in which rats use displacement properties and featural properties in specifying a place suggests to me a modular organization in their spatial representation. One unit of the mind, which I will call the metric frame, encodes *only* the geometric properties in the arrangement of surfaces as surfaces. It encodes the shape of the environment, including the displacement properties in that shape. This module is used to specify the locations of features, including desired objects such as food. Features are not part of the metric frame, but kept in separate modules coordinated with the metric frame via address labels. Each feature carries an address label specifying a location on the metric frame, the address couched in terms of displacement properties. Locations on the metric frame might also carry labels specifying what features are found at the address. It is unclear how different features are divided into modules, but the crucial point is that they are separate from the metric frame used to specify locations in space.

In using landmarks to specify a target place, the rat would usually specify the target only as an address on the metric frame. In normal environments lacking geometric ambiguity, the metric frame can be matched to the perceived world in only one way, and an address on the metric frame unambiguously specifies a location. In environments with rotational ambiguity, featural information must also be used to unambiguously specify a place. The failure to use featural information from other modules would result sometimes in rotational errors.

To speak of separate modules and systems is not to claim that these are necessarily separate stores of information each with its own contents. It might be that all potentially useful information for spatial orientation is stored together in one record, but that different access rules make one kind of information, the geometric, more accessible for navigational purposes. The data cannot decide between the one store or many stores issue, and the terminology of "systems" and "modules" is meant to be neutral on this point.

Featural subsystems

It is unclear how features are used to help specify a place, but the data suggest the following. A target place is still specified as an address on the metric frame. But in addition, some requisite features near the target are 'glued' on. The target must now match specifications on geometric relations to the environmental shape plus local features. That is, not only must the surfaces about the target location line up in the way specified according to its address on the metric frame, but the features near the target must match specifications as well. For spatial orientation, the rat does not use features independently of a geometrically specified location. Features near the target location are checked rather than the overall featural arrangement. The importance of local features is shown in Experiment 2: when the distinctive panels at the correct location and its diagonal opposite were removed, the animals failed to use the remaining features distant from the target to disambiguate geometrically equivalent locations. Local features continued to be used even when the overall featural arrangement is changed: in Experiment 3, the diagonal transposition did not adversely affect performance. But the geometric address at which the food and its local featural information are found must stay the same: when a transformation changed the geometric address of the target features (the affine transformation and reflection used in Experiment 3), performance declined.

Cognitive map and taxon system?

The metric frame perhaps corresponds to what others have considered as the cognitive map (e.g., Menzel, 1978; O'Keefe & Nadel, 1978; Olton, 1982; Roberts, 1984). Both are records of relations among landmarks used to get the animal to desired places. What the present data suggest is that the cognitive map specifies locations primarily by their geometric relations to environmental shape, in particular in terms of displacement properties.

Do the featural subsystems correspond to what O'Keefe & Nadel (1978) have called the cue guidance or taxon system? Both orient the animal towards some distinctive stimulus pattern. Differences in the conditions under which these systems operate, however, suggest that they are distinct. The rats here searched for a featural pattern only at or near a geometrically specified location. In using the cue guidance system, the animal heads towards an object or stimulus pattern irrespective of that object's geometric address. Discrimination learning experiments have shown that the rat can sometimes do this (e.g., Bauer & Lawrence, 1955; Grice, 1948; Lawrence, 1949). The featural subsystems here form a part of a spatial representation system that primarily

specifies places in geometric terms. The limits on using features described above hold when the rat is using features to help specify a place within an environment. Discrimination learning shows that the rat has another mode of using features in which it heads for a featural pattern irrespective of place. The conditions under which each type of system is employed are unclear, but this division makes some teleological sense. To unambiguously specify a place in a normal environment, geometric properties alone suffice. But some objects are desirable irrespective of location. To identify those objects, their featural properties might need to be checked irrespective of where they are found.

Modular spatial representation in mammals?

Do other mammals show modular organization in their spatial representation? In a working memory task, a chimpanzee, for example, can remember for up to 16 pairs of boxes in a ring around them which of the two contains food (Tinklepaugh, 1932). With a little practice, the animals reached accuracies of up to 90%. Further manipulations showed that the positions of the boxes in the room were crucial for the performance, but not the characteristics of the boxes. The animals relied on location in a larger spatial frame (the room) rather than local features (characteristics of the box in which food is put). What is not clear is whether position in the room is specified primarily in terms of geometric relations to the shape of the environment.

The question of whether humans possess a purely geometric module raises issues beyond the nature of our spatial representation. Central cognition in humans is widely held to be non-modular. Theorists of otherwise different persuasions believe that once beyond the perceptual systems, all information available to the organism is accessible in one vast web or network (Anderson & Bower, 1980; Fodor, 1983). A geometric module handles only the geometric information in the spatial distribution of objects and features. It is a theoretical unit of the mind dealing with a subset of the information handled by the whole system. The existence of such a unit makes a system modular by Fodor's (1983) criteria. Modular processes are found in early human vision. For example, Treisman and her colleagues found evidence suggesting that different dimensions of featural information in the visual array are separately processed and then integrated together to form a percept (Treisman & Gelade, 1980; Treisman & Paterson, 1984; Treisman & Schmidt, 1982). The presence of a single feature is easily ('preattentively') detected; detection time does not increase much with the number of distractors. But if an object needs two features from different dimensions to qualify as a target, detection time increases linearly with the number of distractors (Treisman & Gelade,

1980). This suggests that the presence of a single feature can be 'read' directly from the subsystem handling that dimension of features, but that features from different dimensions require an integration process to determine that they go with each other. This process can go wrong under attentional stress, resulting in features from different objects combined wrongly to form an illusory percept (Treisman & Paterson, 1984; Treisman & Schmidt, 1982). Treisman suspects that the integration process works by using a spatial frame (personal communication). Similar to the story of the rat's spatial representation given here, each feature detected carries an address label specifying where it belongs in a spatial frame. Locations on the spatial frame also have pointers specifying which feature of each dimension is to be found there. The integration process checks locations on the spatial frame serially. Do our central records of the spatial distribution of landmarks, like the rat's, show modular organization? The search for systematic errors in remembering places in geometrically symmetric environments gives one methodological tool for investigating this issue.

Comparative spatial cognition

A record of the shape of the environment made up by the arrangement of surfaces as surfaces is not necessary for relocating a place. Evidence suggests that the bee, in the last stage of navigation, relies on featural information alone. Transformation experiments similar in spirit to the ones done here indicate that the bee, in zeroing in on a goal, uses a system of featural templates (Cartwright & Collett, 1982, 1983; Collett & Cartwright, 1983). It takes a panoramic 'snapshot' of what things look like on the retina at the goal. In getting to the target again, it flies so as to minimize discrepancy between present percept and retinal template. The templates used specify what features (e.g., hues) ought to be found in which compass direction, but not the arrangement of surfaces irrespective of features. In contrast to the rat, some aspects of the overall featural arrangement are used. Retinal angles at which features are found are used in the template matching process. Similar to the rat then, displacement properties, this time in the geometry in the arrangement of featural information projected on the retina, are crucial.

Conclusion

The research here shows that the rat records the geometric relations in the arrangement of surfaces as surfaces, the shape of the environment, for navigational purposes. It systematically confuses locations that are geometrically

equivalent but that differ in their relations to other featural properties such as smell and brightness. In the model suggested by the data, the rat, for navigational purposes, uses for the most part a purely geometric module. It specifies a goal as an address, couched in terms of displacement properties, on this featureless metric frame. Featural information such as brightness and smell is stored in other subsystems or modules, with the metric frame serving as the basis for determining what features go where. In using features for navigational purposes, the rat seems to 'paste' requisite features onto the metric frame at the target location. It checks features near the target and not the overall arrangement of features. The rat's spatial representation exhibits modular organization, with different modules within it handling different subsets of the information handled by the system as a whole.

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Résumé

L'auteur a fait effectuer à des rats des tâches de localisation d'emplacements cibles; les rats étaient testés dans un environnement rectangulaire où chaque coin était caractérisé par des panneaux distincts (voir figure 1A). Les rats commettaient une erreur systématique dans les deux paradigmes expérimentaux utilisés (mémoire de travail et mémoire de référence): ils se dirigeaient parfois vers un point situé à 180° de l'emplacement cible par rapport au centre. Dans le paradigme de mémoire de travail, ces erreurs de rotation étaient presque aussi nombreuse que les recherches réussies. Dans ces expériences, la cible et son équivalent rotationnel ont les mêmes relations géométriques, du point de vue des surfaces environnantes, par rapport au reste de l'environnement, mais des relations différentes du point de vue de leurs propriétés non géométriques comme la luminosité ou la texture. Puisqui l'animal commet des erreurs de rotation systématiques, il n'utilise vraisemblablement que les relations géométriques entre la cible et l'environnement, et non les relations non géométriques. D'autres expériences ont montré que les rats peuvent utiliser de l'information non géométrique, mais dans ce cas ils examinent d'abord les caractéristiques autour d'un emplacement géométriquement déterminé, c'est-à-dire un emplacement caractérisé par ses seules propriétés géométriques. Ils ne semblent pas utiliser la disposition globale des caractéristiques non géométriques. Ces résultats suggèrent que, lorsque le rat utilise des points de repère pour s'orienter, il fait appel à un module purement géométrique dont il se sert aussi pour organiser la localisation de données non géométriques.