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Landmark learning and visuo-spatial memories in gerbils

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Summary. 1. The aim of this study is to understand what a rodent (*Meriones unguiculatus*) learns about the geometrical relations between a goal and nearby visual landmarks and how it uses this information to reach a goal. Gerbils were trained to find sunflower seeds on the floor of a light-tight, black painted room illuminated by a single light bulb hung from the ceiling. The position of the seed on the floor was specified by an array of one or more landmarks. Once training was complete, we recorded where the gerbils searched when landmarks were present but the seed was absent. In such tests, gerbils were confronted either with the array of landmarks to which they were accustomed or with a transformation of this array.

2. Animals searched in the appropriate spot when trained to find seeds placed in a constant direction and at a constant distance from a single cylindrical landmark (Fig. 1). Since gerbils look in one spot and not in a circle centred on the landmark, the direction between landmark and goal must be supplied by cues external to the landmark array. Distance, on the other hand, must be measured with respect to the landmark. Tests in which the size of the landmark was altered from that used in training suggest that distance is not learned solely in terms of the apparent size of the landmark as seen from the goal (Fig. 3).

3. Gerbils can still reach a goal defined by an array of landmarks when the room light is extinguished during their approach (Figs. 4, 5). This ability implies that they have already planned a trajectory to the goal before the room is darkened. In order to compute such a trajectory, their internal representation of landmarks and goal needs to contain information about the distances and bearings between landmarks and goal.

4. For planning trajectories, each landmark of an array can be used separately from the others (Fig. 7). Gerbils trained to a goal specified by an array of several landmarks were tested with one or more of the landmarks removed or with the array expanded. They then searched as though they had computed an independent trajectory for each landmark. For instance, gerbils trained with an array of two landmarks were tested with the distance between two landmarks doubled. The animals then searched for seeds in two positions, which were at the correct distance and in the right direction from each landmark.

5. If an internal representation of an array of landmarks is to be used to plan a trajectory, landmarks seen on the ground must be matched to those held in memory. One way in which gerbils do this is by learning properties of individual landmarks, such as their shape, size or surface markings (Figs. 10, 11, 13). For example, gerbils were able to locate seeds defined by a single relevant landmark while ignoring an irrelevant landmark with different features which was placed randomly with respect to the goal.

6. Several experiments (Figs. 4, 12, 13, 14) suggested that, although landmarks may be used independently for computing trajectories, the process of matching landmarks to the gerbil's representation requires a knowledge of the distances and directions *between* landmarks.

7. We conclude that a gerbil's representation of its environment is complete in that it stores explicitly or can compute from what it has stored the geometric arrangement of landmarks and goal. We discuss the possibility that its spatial memories consist of a set of vectors describing the distance and direction from the goal to each landmark (Fig. 18) and consider the advantages and disadvantages of such a goal-centred memory.

Introduction

Many animals are able to find their way back to a place they have previously visited, employing a wide range of navigational techniques to do so (Schöne 1984). One intriguing and widely used method is navigation by means of visual landmarks (insects: Wehner 1981; birds: Vander Wall 1982; Sherry 1985; mammals: Tolman et al. 1946a, b; Morris 1981; Olton 1982). We explore here the way gerbils use visual landmarks to retrieve a goal. Landmarks fall into several functional classes. The first category consists of 'beacons'. A beacon is an object which is so close to a goal that an animal can reach the goal simply by aiming for the beacon. At the opposite extreme are very distant objects like the sun, stars or mountain ranges which appear to remain stationary with respect to each other as an animal wanders about its terrain. Remote 'compass-marks' of this kind can give direction, but they cannot be used to pinpoint a place. Finally, there is the type of landmark with which we are concerned in the present paper. These are objects which are further away than beacons, but still close enough to provide an accurate fix of an animal's position.

In order to return to a place specified by such landmarks an animal must store an internal representation of the spatial arrangement of landmarks and goal, and formulate an appropriate motor program using this information. This general prescription hides the fact that landmarks can be represented and employed in fundamentally different ways.

A representation can be complete in the sense that all the geometrical relationships between objects in an environment are either stored explicitly or computable from information which is recorded in it. An animal with a Euclidean representation of this kind has in principle the knowledge needed to plan routes within that environment. If we can show that an animal plans detailed routes, we can infer that the underlying representation is a rich repository of geometrical information about the environment.

This line of argument leads to the conclusion that human beings must possess a map-like representation of their immediate surroundings. As Thomson (1980) first showed, people can inspect their surroundings from one spot, close their eyes, and then walk accurately towards a goal, detouring around obstacles on the way. People can also view their surroundings, close their eyes, walk some way and then point accurately at an object which they have not seen since they started to move (Pick and Rieser 1982). Such navigational feats need a representation of the environment which encodes the distances and bearings between objects.

Animals with an incomplete representation of their surroundings may be incapable of *planning* routes from starting point to goal, but this need not prevent them from using visual landmarks to reach a goal. Hymenopterans behave as though their representation is two-dimensional. Both ants (Wehner and Räber 1979) and bees (Cartwright and Collett 1983) seem to store a picture or image of an array of landmarks as seen from their goal. This remembered picture does not include distances between landmarks or between landmarks and goal. These insects probably guide their return by moving so as to reduce the discrepancy between their stored and current retinal image. The difference between the two images is used continuously to specify from moment to moment the direction in which the insect should move. The insect does not compute the distance and exact bearing of the goal, but simply which path to take.

On many scales of neural complexity gerbils lie somewhere between humans and hymenopterans and we can ask whether their spatial memories more resemble those of bees or of people. Do gerbils have a representation which contains information about the distances of objects in their surroundings? And how is their representation used? In the 1940's Tolman had already shown that rats have a good memory for places. Over the past decade, interest in the spatial memory of rodents has revived (see Olton 1982; Roberts 1984 for reviews). Studies on rats have revealed that a place can be defined by visual landmarks which are at some distance from that spot (e.g., Suzuki et al. 1980). Furthermore, the return to a place need not be tied to a specific route: a learned goal can be reached from an unfamiliar starting position and by an unfamiliar path (Morris 1981).

Materials and methods

Experimental animals were females from a black-coloured strain of *Meriones unguiculatus* (the Mongolian gerbil) bred in a laboratory colony. We worked with the Mongolian gerbil because it is active during the day (Naumov and Lobachev 1975) and has reasonable visual acuity (~ 1.75 cycles/deg grating acuity at 70 $\mathrm{cd/m^2}$; Baker and Emerson 1983). We used a black strain because the adults appeared greedier than the agouti wild-type, and we chose females because they have a smaller ventral sebaceous gland than males and secrete less sebum. In fact, we saw no scent-marking during the experiments. Animals which were either littermates or kept together since they were pups were housed in groups of 4 or 5 in glass-tanks with sawdust on the floor and hay for nesting material. They were maintained on a diet of rodent food-pellets (Labsure, Expanded Rodent Diet). All the animals in a tank were treated as one experimental group. They were given the same training and the same tests. Training began when the animals were three to four months old.

For economy, groups of animals were used in more than one experiment. The legend to each Figure indicates which animals provided the data for that Figure. With care the use of retrained animals adds little risk of reaching mistaken conclusions, but there is an enormous saving of time. The speed and fluency of animals in our experimental situation improved over several months, although useful data were obtained long before animals reached their peak performance.

Experiments were conducted on the black floor of an approximately circular arena (diameter 3.5 m) inside a light-tight, black painted room. Gerbils were trained to look for a sunflower seed on the floor at a spot defined by an array of one or more conspicuous landmarks also placed on the floor. Black painted granite chips were strewn over the floor to prevent the gerbils from spotting the seed until it was very close. In most experiments the array and seed were moved to a new position between training trials to ensure that the location of the seed was associated with the landmarks and not with other room cues. The few exceptions are noted in the Results. Each animal was given between 6 and 12 individual training trials daily 6 days a week. It usually took about a month (ca. 150 trials) before a gerbil would, on most trials, run to the correct spot soon after its release into the arena. Unless otherwise specified below, the animal was released from a perspex start-box which was transparent except for a black roof. The position of the start-box on the floor was usually varied from trial to trial making it impossible for the animal to follow a constant trajectory to the goal.

The room was illuminated by a single 150 W tungsten filament bulb in a cylindrical aluminium shade hung above the centre of the arena. This bathed the floor in a pool of light and left the walls in shadow. In some experiments gerbils were trained to perform the final part of their approach to the seed in the dark. During the approach the room lamp was turned off (the light decayed to zero in about 60 ms) and at the same moment an infrared source was switched on. The infrared light was made of an enclosed 1,000 W linear filament lamp filtered by a sheet of black Perspex which cut off wavelengths shorter than 725 nm.

After the animals had learned the task, tests were intermingled with training trials in a ratio of about one to six. For a test a gerbil was released into the arena with an array of landmarks but no seed. Tests were conducted either with landmarks in the training configuration, or with some change in the number, size or arrangement of individual landmarks in the array.

A video camera equipped with a wide-angle lens and a 'Newvicon' tube sensitive to infrared and visible wavelengths was suspended 3.8 m above the centre of the arena in order to monitor the animal's behaviour. The gerbil's search path was recorded on video tape for a brief period immediately after the animal's release.

For analysis, the tape was replayed at 1/5th speed. A bright spot was mixed electronically with the video-picture and used to track the gerbil's movements. The position of the spot on the screen was controlled manually by moving a cursor over a digitizing pad. The position of the spot was fed automatically into a computer every fifth frame (every 100 ms). The stored data were later displayed in two forms to give (1) the animal's trajectory to the goal, (2) a plot of how an animal distributed its time within the arena during a series of tests.

Results

1. Gerbils can use landmarks to specify a point in space

A group of gerbils was trained to search for sunflower seeds at a constant distance of 50 cm and at a constant compass bearing from a white cylindrical landmark (40 cm high and 6.3 cm diameter). To ensure that the position of the seed was associated with the landmark, cylinder and seed were translated to a different position in the room before each training trial. A well-trained animal

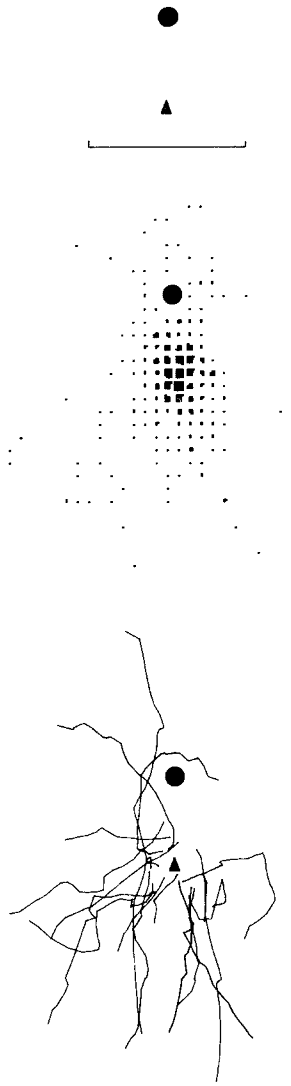

Fig. 1. Search-pattern of one gerbil from cage 5 trained to a seed placed 50 cm from a single white cylinder. Top: plan-view of landmark (●) and reward-site (▲). Calibration bar in this and subsequent Figs. is 100 cm. Landmarks are not shown to scale. Middle: cumulative search-distribution resulting from 21 tests of 60 s duration. In this and subsequent Figs., the animal's position in relation to the landmark-array is given to within a cell 11 cm across and 13.3 cm high. The blacker the cell, the more time the gerbil spent there. Time spent in each cell is expressed as a percentage of that spent in the most visited cell. The latter is filled by 25 dots arranged in a square. In other cells, each dot represents 4% of the peak time. Bottom: 21 trajectories generated by the gerbil when released from different points within the arena. In each case, the gerbil's position was recorded every 100 ms from the time it was released until 1,000 ms after it had entered a small rectangle (22.5 by 25.8 cm) centred on the reward site. The line depicting the gerbil's path joins the recorded positions

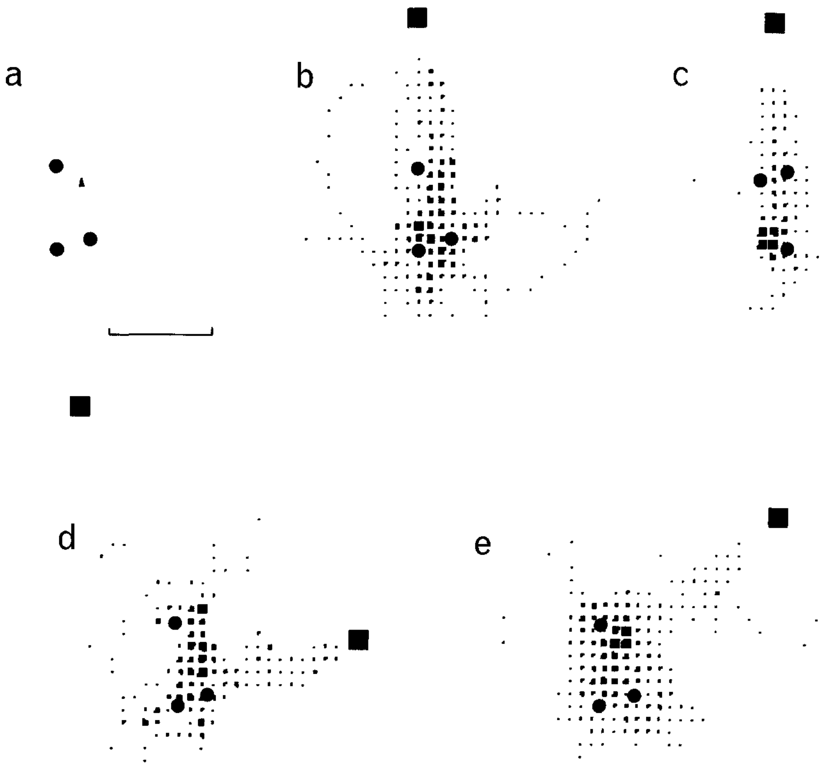

Fig. 2a–e. Search-behaviour of 5 gerbils from cage 7 trained initially to approach a fixed goal from a fixed starting position (**a–d**) and subsequently from all directions (**e**).
a Floor-plan showing start-box indicated by black square, landmarks and goal. Landmarks were three white cylinders 40 cm high and 6.3 cm in diameter.
b Search-distribution resulting from 10 superimposed 15 s tests. The landmarks were displaced from the training position but kept in the same orientation and the start-box was moved to the opposite end of the array.
c Search-distribution resulting from 10 superimposed 15 s tests with both start-box and landmarks displaced and rotated through 180°.
d As **b**, but with start-box placed to the side of the array. Gerbils only search in the correct location in condition c when relation between landmarks and start-box was the same as in training.
e 20 tests of 15 s duration from same gerbils retrained with start-box placed in many different positions with respect to the array. In tests, gerbils always started from the same position. In this and subsequent figures, distributions combine tests from all the gerbils trained in one experiment

will run straight to the expected location of the seed when released into the arena. It does the same in tests with the sunflower seed removed and approaches its goal directly from a variety of starting positions (Fig. 1). After a brief search there and sometimes elsewhere, it goes to the edge of the arena. The path taken was analyzed to show how the gerbil distributed its time in the arena. Peaks in such a distribution (Fig. 1) tell us where the gerbils searched for the seed. In this case the single peak is, as expected, roughly 50 cm from the landmark.

An internal representation of a landmark in the vicinity of an inconspicuous goal can be used to find the goal if it contains information about bearings and distances between the goal and objects in the environment. We begin by asking: What kinds of directional and distance information does the gerbil store?

2. Direction can be given by cues external to the array of landmarks

A single, radially symmetrical landmark cannot on its own define a point on the floor but only an annulus centred on that landmark. The restriction of the gerbil's search to the right position when trained to one landmark means that there must have been another source of directional information. In some circumstances, direction is given by the bearing of a landmark from a fixed starting position. A gerbil foraging from its burrow can use the bearing of a prominent landmark from the burrow as a reference direction. The bearing of a source of food from that landmark can then be learnt relative to this reference bearing. As we will see, gerbils use this directional cue, but since they can also reach a goal directly when released from any direction (Fig. 1), they do not always rely upon it.

To discover whether a constant relation between landmarks and starting position can supply directional information, 5 gerbils were trained to find seeds in a spot defined by three white cylindrical landmarks arranged in a scalene triangle (Fig. 2a). During training, the array of landmarks and reward was kept in a constant position within the room and the gerbils were released from a start-box which was also held in a constant location. Within a few days the gerbils (which in previous experiments had approached this array from a variety of starting positions) ran straight to the seed immediately the start-box was opened. Tests were conducted in which the whole arrangement of start-box and landmark-array was translated and rotated through 180° with the distance between array and start-box varied over about 50 cm. The gerbils continued to run straight to the goal site specified by the landmarks and searched there (Fig. 2c).

This result can be exlained in two ways: (i) the position of the goal is specified entirely by the array of landmarks: (ii) direction is given by the bearing of the landmarks from the start-box. The first possibility was eliminated by the results of tests in which the landmarks were left in the training orientation and the start-box displaced to shift the gerbil's approach path by 90° or by 180°. In these tests the gerbils appeared lost and searched widely within the vicinity of the landmark array (Fig. 2b and d). Thus, when gerbils are given a constant relation between starting position, landmarks and goal, they soon come to depend upon this directional cue and ignore others.

However, when the starting position was varied during training, other directional cues became more salient. The same group of gerbils was trained to the same landmark-array. Array and start-box were translated randomly from trial to trial, both with respect to each other and within the room, with the orientation of the array kept constant. After three weeks of training the gerbils became adept at finding the seed wherever the start-box was placed. In tests, they searched in the appropriate position relative to the landmarks (Fig. 2e).

Thus, gerbils have at least two sources of directional information available to them: (1) the relation between starting position and landmarks (Fig. 2); (2) unspecified directional cues external to the array (Fig. 1, see also Figs. 6 and 7). It will be shown later that, in some conditions, direction between array and reward is specified entirely by the array.

3. Is apparent size the gerbil's only cue to distance?

Gerbils could, like bees (Cartwright and Collett 1983), locate a goal not by recording the distance between landmark and goal in the sense of knowing how many steps it takes to traverse that distance, but by learning how large the landmark appears when the sunflower seed is reached. To find the seed, a gerbil would then move until the size of the landmark on its retina matched the remembered size of the landmark.

If gerbils were to follow this strategy, it would be possible to manipulate where they searched by changing the size of the landmark. 4 gerbils were trained to find a seed at a constant distance from one landmark and were tested with landmarks

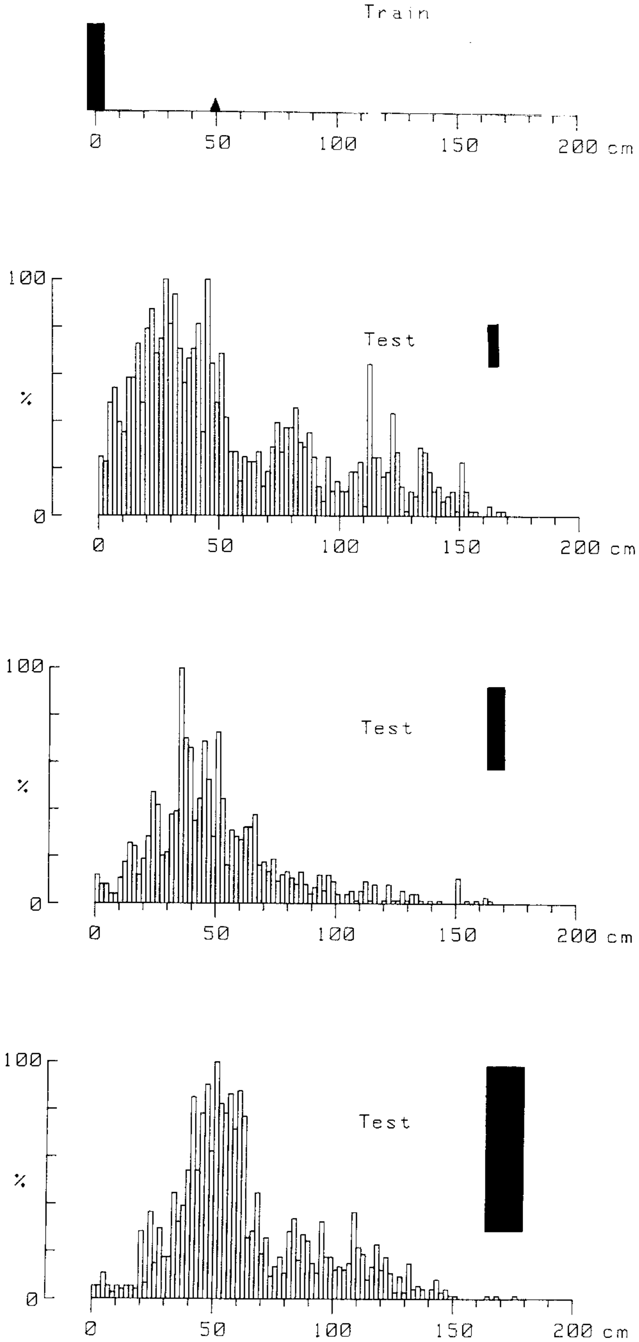

Fig. 3. Searching behaviour of 4 gerbils from cage 5 trained to a seed placed 50 cm from a white cylindrical landmark 40 cm high and 6.3 cm across and tested with landmarks of three different sizes. The two-dimensional search-distributions have been compressed into histograms. Each histogram shows the relative distribution of the gerbils' time within a rectangle 22.5 cm wide and 200 cm long on the floor of the arena, beginning at the landmark and passing through the reward-site. Binwidth 10 cm along the rectangle. Top: diagram of relative positions of landmark and seed during training. Top distribution: 12 superimposed tests with a cylinder 20 cm high and 3.5 cm in diameter. Each test was 60 s long. Middle distribution: 16 tests of 60 s duration with training cylinder. Bottom distribution: 12 tests of 60 s duration with a cylinder 70 cm high and 11 cm diameter. Data from 4 gerbils from cage 5

which were either almost two times bigger or half the size of the training landmark. The position of the search-area remained roughly the same in tests with the larger landmark, but it shifted closer to the cylinder when that was smaller than the one used in training (Fig. 3).

Did gerbils search closer to the smaller landmark just because it was inconspicuous at 50 cm? To answer this question a different group of 4 gerbils was trained to find sunflower seeds 50 cm from the large landmark (70 cm high and 11 cm in diameter) and then tested with the medium sized one. In such tests, the search-area was still drawn towards the cylinder, showing that its displacement was not a result of the landmark being hard to see.

This pattern of results cannot be interpreted simply. Because the search-area remained in about the same position when the size of the landmark was doubled (Fig. 3), apparent size cannot be the only distance cue guiding the gerbil to its goal. Nonetheless, the displaced distribution generated by reductions in landmark size indicates that size is not ignored.

4. Gerbils plan trajectories to the goal

Compelling evidence that a gerbil's spatial representation contains a genuine measure of distance comes from the demonstration that the animal is able to plan trajectories towards a goal and execute them in the dark. Suppose an animal has learned the position of some point on the ground in terms of its relation to a landmark. When placed at some arbitrary distance from this goal, it can compute a vector which defines a trajectory to the goal provided it knows two things: (i) its current distance and direction from the landmark and (ii) how far and in what direction the goal lies from the landmark (Fig. 18). To see how well gerbils plan a trajectory, we examined their behaviour when the room lights were extinguished while they were running towards the goal. If they are able to reach their goal under these conditions, it implies that they planned their trajectory in the light and executed it in the dark.

Five gerbils were trained to leave a start-box and to run straight towards a sunflower seed placed in a constant position with respect to three landmarks arranged in a scalene triangle. The position of the array of landmarks and also the position of the start-box with respect to the array was changed between training trials, but the orientation of the array was kept constant. Once the animals had been trained in the light, they ran straight from the start-box to the seed. In a second phase of training, the room-light was switched off as the gerbil approached the goal. Gerbils usually continued their trajectory and often found and ate the seed in the dark. If they appeared lost, the light was turned on again. During tests the light was extinguished at various times after the gerbil had begun its approach. The position of landmarks and start-box was varied from trial to trial. The gerbil's behaviour was recorded for about 10 s after it had begun its approach.

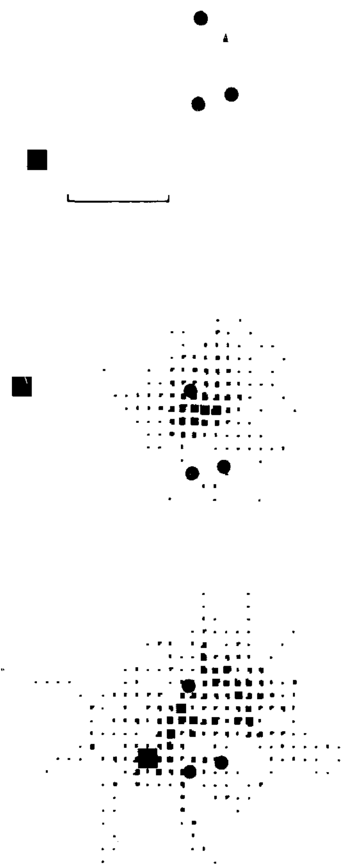

Fig. 4. Search-patterns of 5 gerbils from cage 7 trained to reach their goal in the dark. Top: arrangement of landmarks and reward-site. Landmark at the apex of the triangle was a white cylinder, 6.3 cm in diameter and 40 cm high. Those at the base were an aluminium cylinder 26 cm in diameter and 34 cm high and a white container, 17 by 12 by 27 cm high, both marked with black tape. The bearing and distance of the start-box from goal was varied in training and testing. Middle: search-distribution of gerbils during 23 tests lasting 10 s. The light was extinguished after a gerbil had started its approach. Bottom: search-distribution during 20 control tests. The gerbils were allowed to see the landmarks from the start-box. The light was then extinguished and the start-box was moved close to the landmarks before an animal was released. Data from 5 gerbils from cage 7

The distance between the goal and the gerbil's position when the light went off ranged between 100 cm and 250 cm. The distribution in Fig. 4

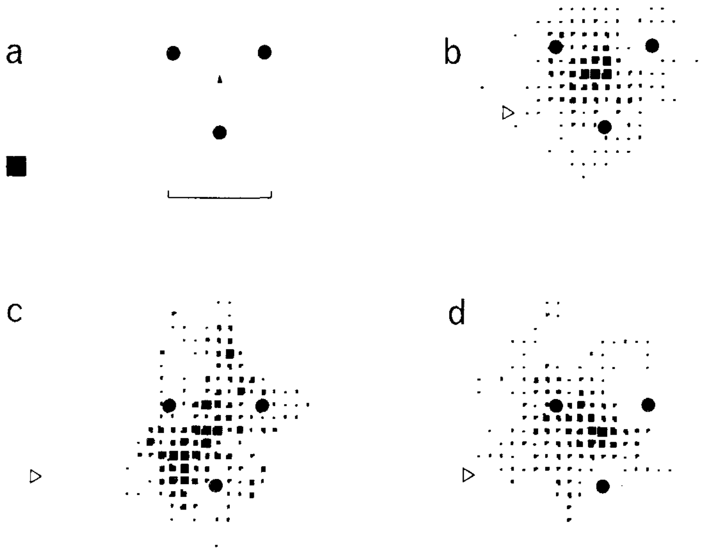

Fig. 5a–d. Search-patterns of gerbils trained to approach an equilateral triangle in the dark from all directions. **a** Floor-plan showing array of three white cylinders (40 cm high and 6.3 cm in diameter), goal and start-box. **b–d** Search-distributions generated when the light is turned off with the gerbil at various distances from the goal
b 21 tests of 10 s duration. The light was switched off when the gerbils were between 60 and 80 cm from goal. Open triangle represents starting point of trajectory in the dark.
c 14 tests; light off with gerbil between 100 cm and 160 cm from goal.
d 16 tests; light off with gerbil between 80 cm and 100 cm from goal. Data from 4 gerbils from cage 9. Search-patterns produced by these gerbils with the light on are shown in Fig. 15

shows that the gerbils' search area is indeed centred on the predicted spot. So we conclude that they can execute a preplanned trajectory in the dark.

Although under infrared illumination the landmarks were undetectable to a human eye, we wished to make sure that they were equally invisible to a gerbil. In one series of control tests we extinguished the room-light while the gerbil was in the start-box. The animal was kept there for about 15 s, while its memory of its starting position decayed, and then released. In such tests, all the gerbils behaved as though they were lost and wandered over much of the room. However, it remained possible that the gerbils would still be able to detect the landmarks when they were in their immediate vicinity. In a second group of control tests, the light was again turned off while the gerbil was in the start-box. The box with the gerbil inside was moved close to the landmarks and only then was the animal released. Although the gerbils were close to the landmarks and moved among them, they still did not search in the correct spot (Fig. 4 bottom).

The previous control suggests that gerbils cannot be guided solely by odours emanating from the landmarks. Nonetheless, such odours might increase the animals' accuracy when they know they are in the neighbourhood of the goal. On some test trials, with the light extinguished during the approach, the normal odours of the landmarks were masked by wrapping them in transparent polythene film. Neither the size nor the position of the search area was altered by this procedure.

A second group of four gerbils was trained in the same way to reach a seed in the dark. The seed was placed in the centre of an array of three white cylinders arranged in an equilateral triangle (Fig. 5). Gerbils performed accurately in this task, indicating that an ability to execute a trajectory in the dark is not limited to a particular arrangement of landmarks.

However, one striking difference emerged in the behaviour of gerbils trained to the two arrays. Test trials were segregated into three groups according to the distance covered in the dark. With the equilateral triangle, the superimposed plot of short trials (60 cm to 80 cm in the dark) was less scattered than that generated by longer trials (100 cm to 160 cm) (Fig. 5). When the gerbils had to traverse a long distance in the dark, they searched both inside and outside the triangle. Perhaps, at a distance, they made mistakes when matching items in memory to the landmarks seen on the ground. The animals trained with the scalene triangle generated peaks which were equally pronounced whether the path covered in the dark was long or short.

These experiments tell us then that a gerbil's visuo-spatial memories do contain distance and direction, and that its memories are map-like in their content and function.

5. Trajectories are computed using information from single landmarks

How do gerbils use their internal representation of an array of landmarks to reach the goal? Our experiments suggest a somewhat surprising but computationally simple answer to this question. It is that trajectories can be planned treating landmarks individually, rather than relying on global geometrical properties of the array.

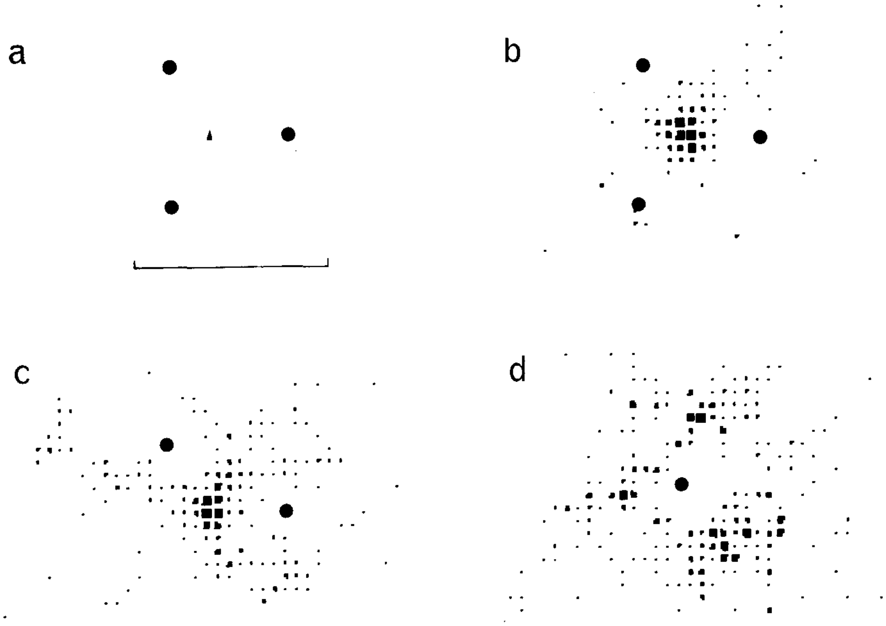

Fig. 6a–d. The removal of landmarks from an array of three. **a** Floor plan of training arrangement. Landmarks were white cylinders 40 cm high and 6.3 cm across. This experiment and that of Fig. 8 were performed in a different room with windows along one wall and a lower ceiling (cell size is proportionately smaller: 7.5 cm across, 8.5 cm high). **b** Search-pattern with training array; 14 tests of 120 s duration. **c** One landmark removed; 8 tests each lasting 120 s. **d** Two landmarks removed; 19 tests. Data came from 3 gerbils from cage 2

Gerbils trained to an array of several identical landmarks and tested with all but one of the landmarks removed searched in several sites. They behaved as though they had identified the solitary, remaining landmark as first one and then another of the elements of the array. Figure 6 shows the search-pattern of gerbils trained to the centre of an array of three landmarks forming an equilateral triangle. With all landmarks present or with one landmark removed, the search-area was restricted to a single site. With two landmarks removed, the gerbil's search-time appeared to be distributed between three areas, one for each of the three possible matches. This pattern of search implies that the gerbil has learnt the distance and direction of each landmark from the goal, and that given just one of the landmarks it can use the information associated with that landmark to find the goal.

The same pattern is seen more clearly in the results of the experiment illustrated in Fig. 7. Another group of gerbils was trained to find a seed to the south of a line connecting two identical landmarks and then tested with one landmark removed. Gerbils searched at the correct distance either to the south-east or to the south-west of the single landmark, treating it sometimes as the western and sometimes the eastern element of the array, with most animals looking in both locations.

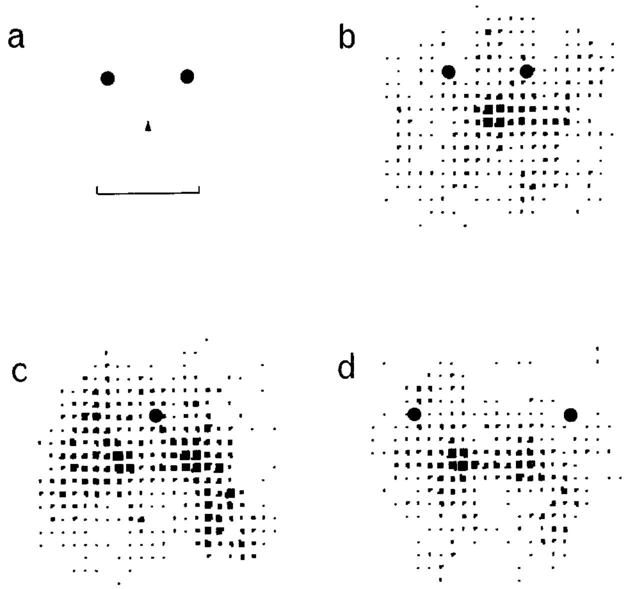

Fig. 7a–d. Transformation of an array of two landmarks. **a** Training arrangement. The two landmarks were white cylinders 70 cm high and 11 cm in diameter. **b** Search pattern with training array; 20 tests of 30 s duration. **c** One landmark removed; 20 tests. **d** Distance between landmark doubled; 21 tests. Data came from 4 gerbils from cage 5

These tests show that animals given just one out of an array of several landmarks can still plan trajectories. Tests in which the two landmarks were placed further apart than they were in training suggested further that it may be the gerbil's normal practice to compute a separate trajectory for each landmark independently of others in the array. When the distance between the two landmarks was doubled, the gerbils searched in two discrete areas, at the appropriate distance and bearing from each landmark (Fig. 7). This distortion of the geometry of the array did not change the way in which gerbils used the information supplied by individual

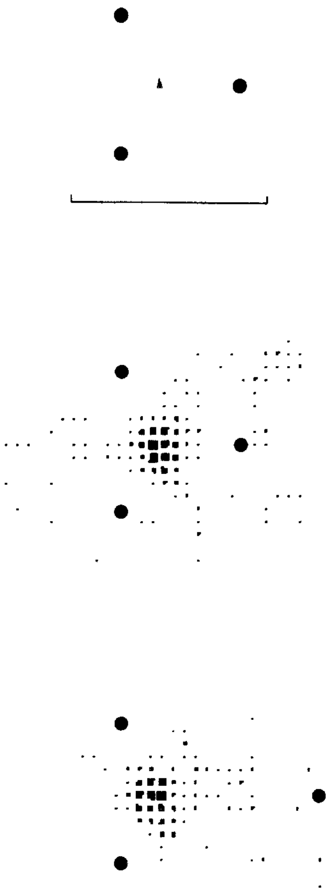

Fig. 8. Distortion of an array of three landmarks. Top: training arrangement. Middle: search-distribution with training array; 20 tests of 120 s duration. Bottom: search-distribution when the distance of one landmark from the goal was doubled. 12 tests. Data from 3 gerbils from cage 2

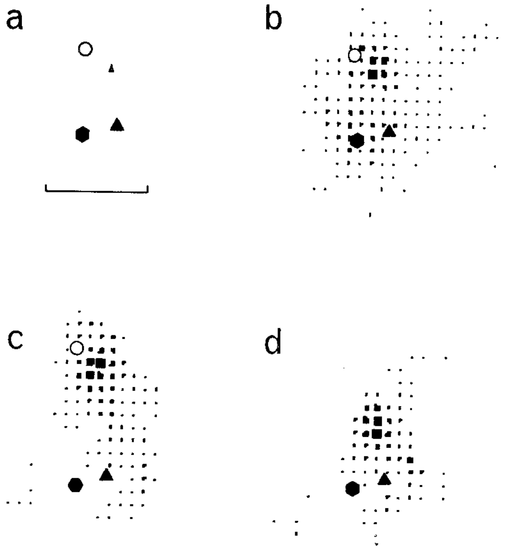

Fig. 9a–d. Transformations of an array of three landmarks. **a** Training arrangement. Landmark nearest goal is white cylinder (40 cm high and 6.3 cm in diameter) landmarks at base of triangle are aluminium cylinder decorated with black tape (26 cm high and 34 cm in diameter) and white cylinder (70 cm high and 11 cm in diameter). **b** Distribution with training array; 14 tests of 30 s duration. **c** 20 tests in which the distance between base and apex of triangle has been doubled. **d** 15 tests with landmark at apex removed. Data from 5 gerbils from cage 7

landmarks. Although the goals specified by the two landmarks disagreed, there was no spatial averaging. The gerbil searched in the place defined by one or other landmark, but not in an intermediate location.

The results of this experiment also imply that the gerbils know which is the eastern and which the western landmark. When the array was expanded, the animals searched predominantly just to one side of each landmark – to the south-west of the eastern one and to the south-east of the western one. Had the landmark not been identified by its position relative to its partner, each landmark should have generated two peaks, as happened in tests with a single landmark. It is important to make sure that the search-pattern gerbils generated when confronted by the expanded array was not influenced by the walls of the arena. For this reason, gerbils were tested with one end of the expanded array placed toward the centre of the arena. The search-pattern in these tests resembled closely that found when the midpoint of the test array was in the centre of the room. It is thus unlikely to be the edge of the arena which prevents the expression of a second peak.

Although individual landmarks may be treated independently when trajectories are computed, this is not the case when it comes to choosing between several possible trajectories. In one experiment, gerbils were trained to the centre of an equilateral triangle formed by three identical landmarks. They were tested with the distance between just one of the landmarks and the centre doubled. Almost all of the animal's search time was spent at the site defined by the two landmarks which retained their normal relationship (Fig. 8). The position indicated by the outrider was ignored. The gerbil is thus equipped with a useful procedure for deciding between discrepant solutions. When most of the landmarks agree in specifying the same goal, with just a few pointing to other sites, the chances are that the majority view is correct and that the additional possibilities result from mistakes in computation or from disturbances to the environment.

A rather different decision rule is that some landmarks are given greater weight in guiding an animal's path than others. Gerbils trained to the scalene triangle illustrated in Fig. 9 were tested with the long axis of the triangle expanded by a factor of two. The animals searched consistently in the position defined by the landmark which normally lies closest to the reward site. This does not mean that the two other landmarks had been ignored during training. When the landmark closest to the reward-site was removed, the animals looked in the spot defined by the remaining two (Fig. 9). The advantage of weighting close over distant landmarks is that the former define the goal more accurately than the latter.

Taken together, these results dispose of any lingering possibility that gerbils rely principally upon the bearing of landmarks with respect to each other to guide them to their goal. On the contrary, with both expanded and truncated arrays, gerbils search at the right distance and at the correct bearing from individual landmarks.

6. Matching the representation to the world

Before a stored representation of an array of landmarks can be used to compute a trajectory, the representation must be matched to what the animal sees. This process can be divided into two components. First, the representation and current view must be oriented congruently so that a reference direction in the animal's head coincides with a reference direction on the ground. The experiments of this section will show that, in addition to the directional cues discussed earlier, the array itself can provide compass information.

The second part of the process is to match individual landmarks in the representation to individual landmarks seen on the ground. This means landmarks must be identified. In principle, a landmark can be recognised by particular features it possesses, like its shape or colour, or by its geometrical relation to its neighbours in the array. Thus, a landmark might be labelled, often unambiguously, in terms of the bearings and distances to its two nearest neighbours.

We have used three different methods to see whether gerbils can recognise features of landmarks. In the first experiment, animals were trained to find seeds in a constant direction 50 cm from either a black-striped metallic cylinder 34 cm high and 26 cm in diameter or from a white cylinder 70 cm high and 11 cm in diameter. When trained to one of these cylinders, the other irrelevant cylinder was also present. From trial to trial, the two were moved randomly with respect to each other so that no useful information could be derived from the irrelevant cylinder. For testing, relevant and irrelevant cylinders were placed in standard locations, with the positions of the two cylinders interchanged on alternate tests. The gerbils searched more in the position specified by the relevant than in the equivalent spot defined by the irrelevant landmark, so revealing that they are able to distinguish between the two landmarks (Fig. 10).

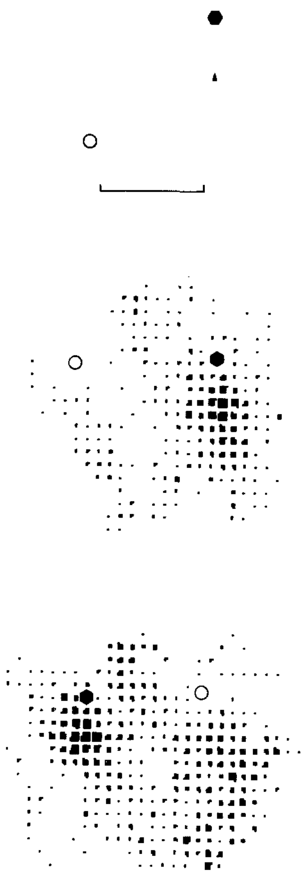

Fig. 10. One relevant (●) and one irrelevant (○) landmark. Top: training arrangement. Seed is placed in a constant position with respect to an aluminium cylinder (26 cm high 34 cm in diameter); position of white cylinder (70 cm high and 11 cm diameter) is varied with respect to aluminium one. Middle: Search-distribution generated by 11 tests lasting 30 s. Aluminium cylinder on right. Bottom: as above but with aluminium cylinder on left. Data from 4 gerbils from cage 5

The second experiment has a dual role. It shows in a very different way that gerbils identify individual landmarks and use this information to locate the goal. It also demonstrates that the position of the goal can be specified completely by the landmark array without any extra cues to direction. A different group of gerbils was trained to a spot defined by a white cylinder (40 cm high 6.3 cm wide) and the same metallic cylinder. The landmarks were separated by a constant distance. After each training trial the configuration of landmarks and seed was rotated and displaced. Gerbils should only restrict their search to the correct site, if they

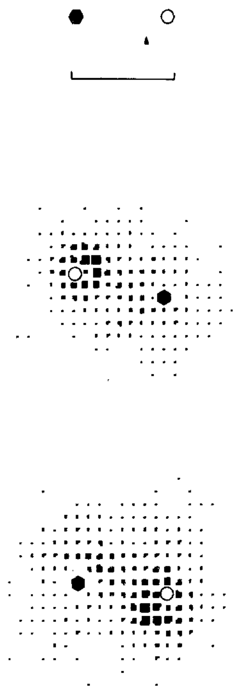

Fig. 11. Rotating an array of two distinguishable landmarks. Top: training arrangement. Landmark near to goal is white cylinder (70 cm high and 11 cm in diameter), other landmark is an aluminium cylinder (26 cm high and 34 cm in diameter). Configuration of landmarks and seed is rotated and translated after each training trial. Bottom: search-patterns with array in two orientations. Each distribution consists of 20 tests of 30 s duration from 5 gerbils from cage 7

are able to distinguish between the two cylinders. Tests were performed with the array in two standard orientations 180° apart: Gerbils searched in the appropriate spot so confirming their ability to recognise these landmarks (Fig. 11).

This result suggests also that the gerbil extracts directional information from the array. To see why, consider what would happen if the array did not supply direction. Suppose a gerbil knew no more than the distance of the goal from the closer landmark, it would then search in an annulus around the white landmark. If it knew the distance from both landmarks to the goal, each landmark would define an annulus and the gerbils would search at the two points of intersection of these annuli. A single peak in the search-distribution of Fig. 11 means that the gerbil knows some geometric property of the array, such as the equivalent of the angle α in Fig. 12.

The two experiments just described were designed so that gerbils could only locate their goal unambiguously if they attended to the features of individual landmarks. The last experiment asks whether landmark-features are noticed when there is sufficient geometrical information for the goal to be reached even if features of individual landmarks should be ignored.

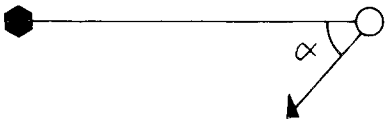

Fig. 12. Tests with rotated arrays of landmarks imply that gerbils must know the direction of the goal relative to the geometry of the array as indicated by the angle α

Gerbils were trained to find seeds at a site specified by the metallic cylinder and a 70 cm high white cylinder. The landmarks were again separated by a constant distance during training, but in this case the orientation of the array in the room was kept constant (Fig. 13). The array was translated between each training trial. Gerbils were released from a start-box which was placed variously, sometimes on one side and sometimes on the other side of the line joining the two landmarks. Initially, animals found this task difficult, often looking for the seed in the equivalent spot on the wrong side of the line. But, when tested after several weeks of training, they searched mostly in the correct place (Fig. 13).

They were also tested with (a) the aluminium cylinder by itself and (b) the positions of the two landmarks interchanged. Gerbils presented with the aluminium cylinder on its own searched in the appropriate position from that landmark, indicating (1) that they had identified it correctly and (2) that external directional cues defined the bearing of the goal from the landmark.

When the positions of the landmarks were reversed, gerbils looked predominantly in the mirror symmetric spot from the goal (Fig. 13). This result confirms that the two landmarks are distinguishable from each other. It shows also that the bearing of the goal from a landmark can be specified by intrinsic properties of the array. The gerbils behaved as though they knew the equivalent of the angle α in Fig. 12 and in this test used it in preference to room cues in specifying the goal. Thus, when array-bound and external directional cues conflicted, array-bound cues predominated.

7. *Some geometrical properties of an array are recognisable at a distance*

So far we have shown that gerbils learn the distances and bearings of individual landmarks from the goal. The final two sections are concerned with the gerbil's knowledge of geometrical relations between landmarks.

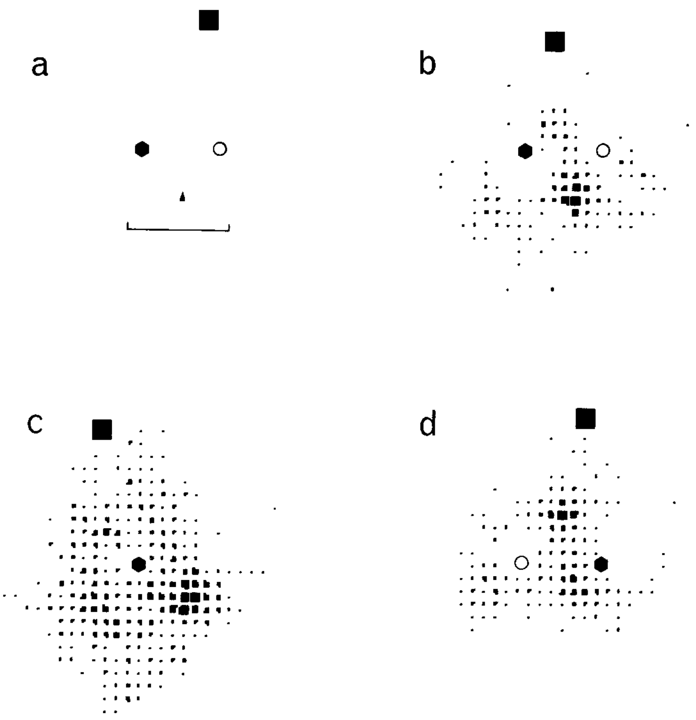

Fig. 13a–d. Transformation of an array of two distinguishable landmarks.
a Training arrangement. Left landmark is aluminium, cylinder; right landmark white cylinder (70 cm high 11 cm in diameter). Start-box is placed in various positions 'above' or 'below' the two landmarks.
b 12 tests lasting 30 s with training array.
c 16 tests with one landmark removed.
d 16 tests with order of landmark reversed. In **b–d**, half of the tests were performed with the start-box above the landmarks and half with the start-box below. Data from 4 gerbils from cage 10

Gerbils were trained to find seeds in the centre of an equilateral triangle formed by three identical cylinders and kept in a constant orientation. After each training trial, the start-box and array were moved to a new position within the room. Tests were conducted either with the triangle in the training orientation or with it rotated through 60°. In both cases the gerbils searched initially in the centre of the array. However, with the rotated triangle, they soon left the centre and often looked briefly for the seed at any of three locations outside the array, producing a search-distribution with a principal central peak and much smaller peripheral ones (Fig. 14).

To account for these results, we must assume that the direction of the goal from each landmark is specified by array-based cues, as well as by cues extrinsic to the array. When the triangle is rotated, the two sets of cues conflict. Array-bound cues indicate the goal to be in the centre of the array, while external cues show the goal to be outside, as Fig. 15 explains. Thus, when the gerbils first approached the rotated triangle, they were guided entirely by array-based cues. In order to search inside the triangle, the gerbils must know the relative positions of all three landmarks.

Do array-based cues predominate when the gerbil is at a distance from the array? To answer this question directly, we accustomed the same group of gerbils to approach the equilateral triangle in the dark. In both training and test trials gerbils were released from a start-box placed anywhere in the room. Once an animal was launched on its approach, the light was extinguished and the trajectory completed in the dark. In tests, these gerbils made for the centre, whether the triangle was in the training orientation (Fig. 5), or rotated through 60° (Fig. 14d). With the landmarks rotated, the trajectory must have been *planned* using directional cues derived from the array.

If presented with an alternative, gerbils preferred to search in an array in which both array-based and external directional cues matched those experienced during training than in one where only the array-based cues were correct. Gerbils were trained to the centre of an equilateral triangle which was kept in one orientation. They were then tested with an array of four landmarks arranged to provide a choice between a triangle in the training orientation and one rotated through 60°. The animals searched for much longer in the correctly oriented triangle where both sets of directional cues were correct than in the other (Fig. 16).

8. Gerbils can learn two landmark arrays simultaneously

Another way to discover whether gerbils learn the geometrical relations between landmarks within an array is to see if they can distinguish at a distance

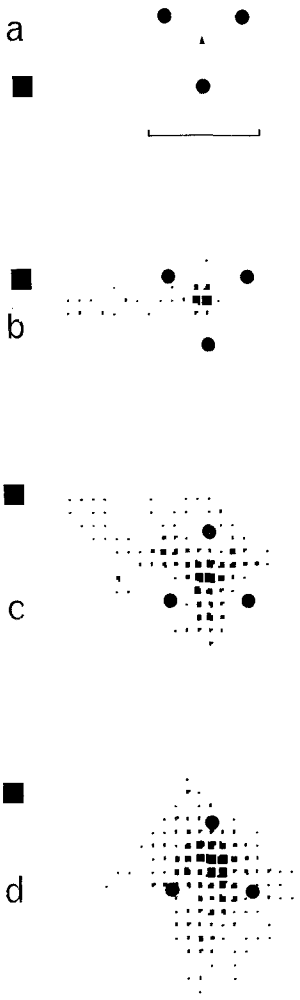

Fig. 14a–d. Rotation of an equilateral triangle. **a** Orientation of training array showing start-box, landmarks and goal. Landmarks were white cylinders (40 cm high 6.3 cm in diameter). **b** Search-distributions in the light resulting from 4 tests of 30 s duration with array in training orientation. **c** Search-distribution in the light resulting from 14 tests of 30 s duration with array rotated through 60°. **d** Search-distributions in the dark with array rotated through 60°. Light was extinguished when animal was between 60 cm and 100 cm from goal; 31 tests of 15 s duration. Data given by 4 gerbils from cage 9

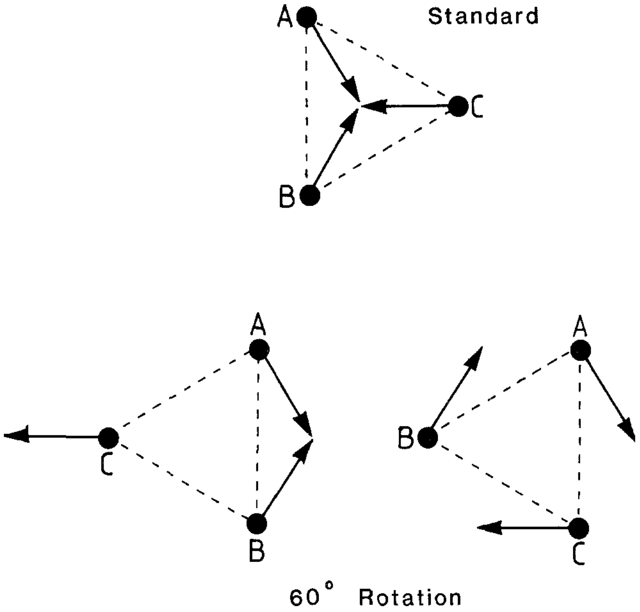

Fig. 15. Schematic account of why external compass cues should lead a gerbil trained to the centre of an array of three landmarks to search outside the array when it is rotated. The goal can be defined by its direction and distance from each landmark. These vectors indicating the goal are shown by the arrows pointing away from each landmark. Each landmark on the ground must be matched to one in the gerbil's representation. When the array is rotated, possible goals will always lie outside the array, however, the two sets are paired. Two out of six possible matches are illustrated

between two arrays of landmarks which differ only in the way the landmarks are arranged. Accordingly, we trained gerbils to search both in the centre of an equilateral triangle formed by three similar landmarks and outside a scalene triangle formed by rearranging the same three landmarks.

Animals were trained initially for several weeks with each array by itself. After this phase, one or two training trials with the scalene triangle was followed by one or two trials with the equilateral triangle. The orientation of each triangle was kept constant, but its position within the room was varied. Animals were tested with one or other array present. A test with the equilateral triangle was always preceded by a training trial with the scalene triangle, and vice versa. In tests, animals searched in the correct location, thus showing that they distinguished between the two arrays (Fig. 17a). However, when the equilateral triangle was rotated through 60°, the gerbils' behaviour was disrupted: the animals searched widely in the vicintity of the landmarks. Another group was therefore trained with the equilateral triangle oriented in a different direction. This group also distinguished between the two triangles, but less cleanly than the first (Fig. 17b). It was clear from training trials that animals occasionally confused the arrays and ran directly to the wrong goal.

In the final stage of the experiment, the room light was extinguished before the animal arrived at the goal. Under these conditions the gerbils, as before, searched mostly in the centre of the equilateral triangle, but in tests with the scalene triangle they did not look consistently in the correct spot (Fig. 17c). Thus, although they can distinguish between the two arrays, it is not clear that they can make this distinction before they are close to the goal. Consequently, these experiments do not tell

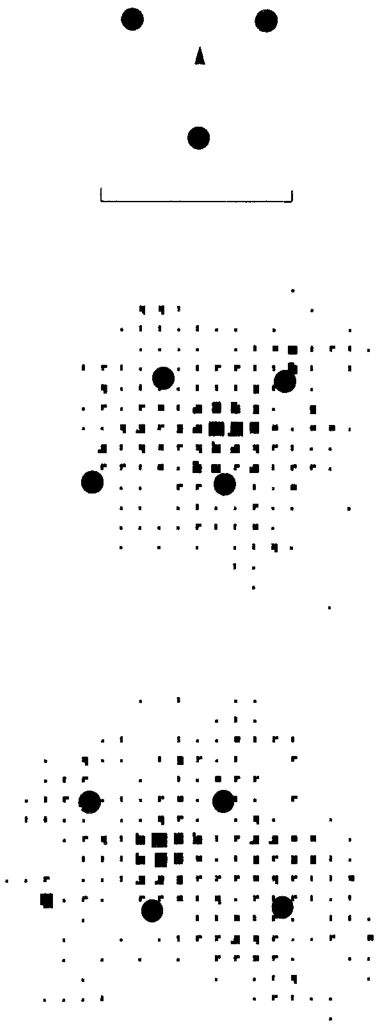

Fig. 16. Search-distributions produced by gerbils trained to find seeds at the centre of an array of three landmarks and tested with an array of four landmarks. Top: training arrangement. Middle: distribution resulting from 16, 30 s tests with 4 landmarks. Bottom: as above, but with landmarks in a different configuration. Data from 4 gerbils from cage 10

us whether gerbils learn geometrical relationships between landmarks. It remains possible, though perhaps unlikely, that each array is recognised by the bearings and distances of individual landmarks as seen from potential reward-sites.

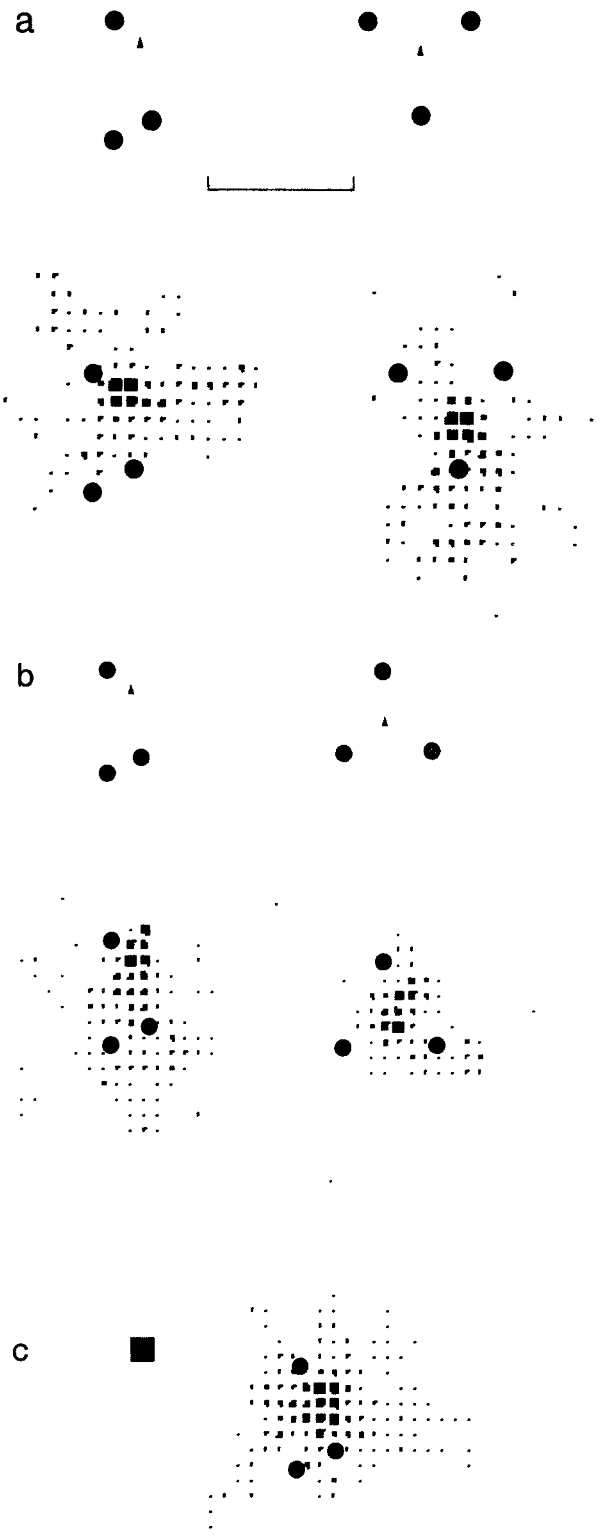

Fig. 17a–c. Simultaneous training to two arrays of landmarks. **a** Top: training arrangement. On different trials gerbils look for a seed placed either in the centre of an equilateral triangle made by an array of three white cylindrical landmarks (40 cm high and 6.3 cm in diameter) or close to the apex of a scalene triangle formed by the same three landmarks. Bottom: search-distributions generated by 20 tests of 30 s duration with the scalene triangle and 20 tests with the equilateral triangle. Data from 4 gerbils from cage 10. **b** Similar experiment with the equilateral triangle in a different orientation. The animals were released from a start-box placed at different distances and in different directions from the array. Search distribution superimposes 20 tests of 10 s duration from 5 animals from cage 7. **c** As **b** but light extinguished when gerbils were at least 30 cm from goal. 36 tests lasting ca. 10 s from 3 gerbils from cage 7

Discussion

1 What do gerbils learn?

These experiments lead to several conclusions about a gerbil's memories of the geometrical relationships between a set of landmarks and a goal. Most notably, the animal's ability to execute a trajectory in the dark means it must remember (or be able to compute from what is has stored) the distances between landmarks and goal and the directions of the landmarks from the goal. In order to plan a trajectory, it is not enough to remember distances in terms of cues like apparent size or binocular disparity or motion parallax. The information must be in a form which makes it possible to compute the length of a trajectory. This means storing something which is equivalent to a real, measured distance. In this respect, a gerbil's representation of landmarks surrounding a goal is very different from that of hymenopterans.

The computation of a trajectory also requires that the gerbil knows its current distance and direction from the landmarks. In other words, the gerbil needs two vectors to plan a route: a seen vector describing the animal's position with respect to a landmark and a stored vector which gives the position of the goal with respect to that landmark. The gerbil can then compute a direct path to its goal by taking the difference between the two (Fig. 18). This simple scheme made us ask whether spatial information about goals and landmarks might not be stored in the form of such vectors.

In a representation of this kind, the memory of a single goal consists of a set of vectors, one for each landmark listing the bearing and distance from the goal to that landmark. Balda and Turek (1984) have made a similar proposal in suggesting that birds remember a cache of seeds in terms of its distance and direction from a prominent object. The principal advantage of such a vector representation is the ease with which information in memory can be combined with current visual input, for both are in terms of the distance and direction of objects from an observer. Moreover, if the ability to store visual information evolved in parallel with the visual system, we would expect memory and immediate visual input to use a common code.

The more usual suggestion (e.g., O'Keefe and Nadel 1978, p. 94) is that a mammal's representation of its environment is analogous to a map in a Cartesian coordinate system. The position of each landmark and goal is stored as a pair of coordinates. The position of the animal must also be specified on such a map. One way of doing so is to place the animal at the origin of the coordinate system so that the values assigned to landmarks and goal change as the animal moves within the environment. Alternatively, the animal's coordinates might shift and those of external objects remain fixed.

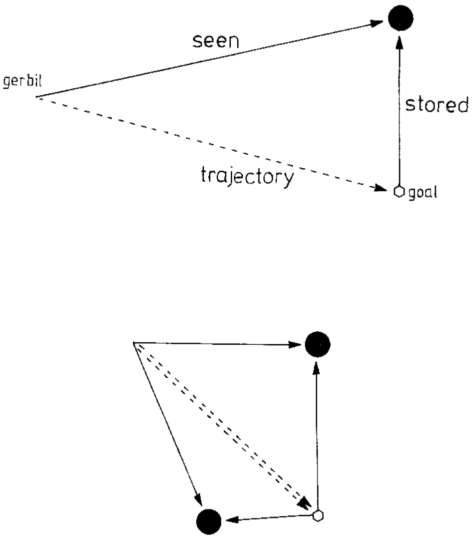

Fig. 18. The use of vectors to plan a trajectory. Top: trajectory is specified by the difference between the seen and stored vectors associated with one landmark. Bottom: When there are two or more landmarks, a separate but coincident trajectory is specified by each

While a vector representation wins on grounds of computational ease, it may lose on economy of storage. Suppose a gerbil has many caches of food within an environment. It will need a different set of vectors for each. The total number of vectors is then the product of the number of landmarks and the number of caches. In comparison, a Cartesian map requires just one set of coordinates for each landmark and one for each cache. In order to plan routes from cache to cache, memories of different caches must be related to each other. In a Cartesian representation no provision need be made for this. In a vector representation some cross-referencing would be needed so that a landmark can be identified as the same from one set of vectors to another.

Behavioural experiments cannot easily decide whether the gerbil uses one of these schemes or indeed something different. The problem is that if the animal knows the distance and direction from the goal to every landmark, it has in principle a complete record of the geometry of the arrangement of goal and landmarks. It then could, given the right machinery, compute any spatial property of an array of landmarks, such as the bearings and distances of landmarks from each other. Obviously, exactly the same properties can be computed from a Cartesian representation. Thus, if the animal's representation is complete, it is hard for an observer to know whether a given geometrical property of the array is stored explicitly or computed from information in the representation.

2 How are spatial memories used?

Tests which bear on this question are those in which landmark-arrays have been expanded or truncated. In such tests, gerbils behaved in a way which is consistent with the hypothesis that they treat each landmark independently when planning a path to the goal and formulate a separate trajectory for each landmark in the array. With no interaction between landmarks, computational problems are kept to a minimum. In an undisturbed world, all the trajectories provided by the set of landmarks will coincide and point to the same place (Fig. 18). Such a collection of redundant solutions has several uses. It provides checks on the accuracy of the computations. If all trajectories are alike, the gerbil can be very confident that they point to the correct spot. Redundant trajectories can also help remove any confusions which may be introduced by displaced or added landmarks. All the gerbil need do is follow coincident trajectories which lead to the same place and ignore outriders.

Before trajectories can be computed, the animal's internal representation must be matched to what it currently sees. Matching is more complex than planning a trajectory because during this process landmarks can no longer be treated independently from each other.

Matching can be separated into two components. The first is that of orienting the representation correctly. The animal must know its direction with respect to the constellation of landmarks and goal. We have identified three ways in which gerbils do this. (1) When they approach a goal specified by a fixed landmark from a constant starting position, the bearing of the landmark to the goal is defined by the bearing between landmark and starting position. (2) When the array has a constant compass bearing, but the goal is reached by a variety of routes, direction can be defined by 'compass' cues which are external to the array. In a natural environment compass information could come from distant visual landmarks or from a variety of non-visual cues. But we haven't examined what cues were used in the present experiments. (3) When both the animal's approach direction and the bearing of the array are varied, the animal can in some circumstances obtain directional information from the array itself (Figs. 11 and 14). To do this a gerbil must know something about the geometrical relations between landmarks.

The second component is that of matching individual landmarks in the representation to those on the ground. One method the gerbil uses is to label individual landmarks in terms of properties like their shape, size or surface markings. In all likelihood, the geometry of the array is also used to distinguish individual landmarks from each other. For instance in Fig. 2e, the landmark at the apex of the triangle could be identified as the one furthest away from other members of the array.

Thus, both components of the matching process seem to demand that gerbils can recover from their representation the spatial relations between landmarks. However, if trajectories are computed using landmarks independently of each other, information about spatial relationships between landmarks may be ignored once matching is achieved. This scheme is far from the whole story and is presented only as a working hypothesis. Our data are undoubtedly consistent with a range of more complex models.

Since gerbils can plan trajectories towards a goal when they are some way from it, landmarks must be recognisable at a distance. Is recognition at a distance achieved by relying on a single memory formed at the goal or do gerbils learn what an array looks like from different positions? Suppose the only available spatial memory is formed at the goal. When the gerbil is far away, it may have difficulties in matching landmarks in its representation to those on the ground, because a landmark or the pattern of the array appears strange when seen from an unfamiliar viewpoint. Although by no means conclusive, the experiments illustrated in Figs. 13 and 14 hint that gerbils may learn the appearance of the array of landmarks from several positions and use this information for matching.

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