

LANDMARK STABILITY: STUDIES EXPLORING WHETHER THE PERCEIVED STABILITY OF THE ENVIRONMENT INFLUENCES SPATIAL REPRESENTATION

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Summary

To investigate whether spatial learning complies with associative learning theories or with theories of cognitive mapping, rats were trained in three experiments exploring the effect of variations in spatial predictive relationships.

In experiment 1, it was found that making one of two landmarks the sole spatial predictor of reward, by varying the spatial relationship between reward and other cues, reduced the control over search exerted by that landmark compared with that observed when the landmark and context cues were both reliable predictors of reward location. This requirement for landmark stability rather than predictive power appears to contradict results obtained in conventional conditioning paradigms. Discrimination learning was unaffected, suggesting a dissociation between discrimination and spatial learning with respect to the influence of geometric stability. Further experiments used arrays of both single and multiple landmarks. Experiment 2 revealed that the stability of a

single landmark improved accuracy of search, but also showed that local stability between a pair of landmarks that moved around the arena together was sufficient to support spatial learning. Experiment 3 examined landmark stability using fixed directional cues in the absence of vestibular disorientation. This also revealed a relative advantage of stable landmarks, but animals presented with a landmark that moved from trial to trial did show some evidence of learning.

Parametric manipulation of landmark stability offers an intriguing way of influencing the process of spatial representation and thus understanding better the processes through which egocentric representations of perceived space are transformed into allocentric representations of the real world.

Key words: landmark stability, perception, spatial representation, cognitive mapping, associative learning.

Introduction

A widely accepted theoretical approach to the study of animal learning is based on the assumption that learning can be adequately described by specifying the strengths of associations between events (or their features) and the rules governing changes in associative strength (Dickinson, 1980; Mackintosh, 1983). However, its applicability to spatial learning has been disputed on both empirical and theoretical grounds, with several authors favouring an account of spatial learning in terms of cognitive mapping (Gallistel, 1990; O'Keefe and Nadel, 1978; Worden, 1992). For example, O'Keefe and Nadel (1978) draw a sharp distinction between spatial and associative learning, arguing that the former occurs very rapidly (e.g. in one trial), is non-associative, depends upon the integration of information into maps and upon processing in brain regions different from those subserving associative learning. However, some of their arguments for ascribing a special status to spatial learning may be questioned. Features thought to distinguish spatial from associative learning, such as rapid learning or predispositions to use certain types of cues, are shared by taste aversion learning. While taste aversion learning was characterised as a specialised learning process at

one time (Rozin and Kalat, 1971; Shettleworth, 1972), it is now widely accepted as a phenomenon that can be understood in associative terms (Revusky, 1977; Dickinson, 1980).

It is not immediately obvious how to compare the approach suggested by animal learning theory to the study of spatial learning with that of cognitive mapping. Should spatial learning be thought of as involving classical or instrumental conditioning, both or neither? How does one achieve satisfactory stimulus control in the spatial domain? A promising approach is to concentrate on areas where associative learning theories and cognitive mapping theories make specific and differential predictions. Diez-Chamizo *et al.* (1985) tested the cognitive mapping theory's assumption that locale and taxon information are independent (the locale system creates a map of the environment, the taxon system uses orientation and guidance strategies, i.e. heading for a beacon or following extended cues such as rivers). They identified O'Keefe and Nadel's locale system with extramaze cues, the taxon system with intramaze cues, and reported that blocking can occur between these two sets of cues. This indicates that, at some level of processing, they must interact.

Diez-Chamizo *et al.* (1985) and March *et al.* (1992) also demonstrated overshadowing between intra- and extramaze cues. While these results raise a question about the independent status of the putative locale and taxon systems, the identification of these systems with the exclusive processing of extra- and intramaze cues, respectively, can be questioned. We see no reason why spatial learning cannot occur amongst intramaze cues. A more specific prediction of cognitive mapping theory is that blocking may not occur *within* the locale system because all relevant cues should be incorporated into the animal's map once they have been explored. To our knowledge, this prediction has not been tested. O'Keefe and Nadel (1978) have also suggested that overshadowing may not occur within the locale system, viz: 'Incorporation of information about stimuli occurs in a non-incremental fashion' (p. 95). However, a recent study by Spetch (1995) has shown overshadowing in pigeons based on relative, not absolute, proximity to a goal between otherwise equivalent landmarks on a touch screen.

Our approach has been to consider the possibility that spatial learning can be understood within an associative framework, but that it may not obey all the principles that have been identified in conditioning experiments conducted to date. Contingency has a central role in modern accounts of associative conditioning. Rescorla (1968) found that the associative strength of a conditioned stimulus depends on how well it predicts the unconditioned stimulus. Wagner *et al.* (1968) found that when the correlation of a target stimulus with the unconditioned stimulus is held constant its associative strength is inversely related to how well other stimuli predict the unconditioned stimulus. This relative validity of a cue in comparison with other cues and the degree of correlation between two events are, therefore, important determinants of associative strength. By analogy, a simple associative account of spatial learning predicts that making a landmark the sole *spatial* predictor of reward, achieved by keeping constant the spatial relationship between the landmark and reward while varying all other relationships, should maximise the control exerted by this landmark over the location of search. The landmark should have less control in a condition where other cues are also potentially reliable predictors of reward location. In both cases, the probability of reward given the presence of the landmark would be held the same; all that would change is its relative spatial validity. In contrast to this associative account, stimuli might only be included in a cognitive map if they are geometrically stable with respect to other cues the animal can perceive, viz: '...such variability could block the locale system from directing behaviour and bias the organism towards other hypotheses' (O'Keefe and Nadel, 1978, p. 95). Cognitive mapping theory predicts, therefore, that learning the relationship between an individual landmark and reward would be most effective when several landmarks, or a landmark and distal directional cues, form a stable geometric framework.

Principal features of the training protocol

Our experimental method has been inspired by the work of Collett *et al.* (1986) who, using gerbils trained to search for sunflower seeds, showed that these animals could learn to search accurately at a particular distance and direction from radially symmetrical landmarks. Although their study (and several others) varied spatial relationships during either a training or test phase, none has been designed to explore the effects of such variability on the acquisition of a spatial representation. Our training protocols are characterised by the following general features.

(1) We use a large open-field arena in which rodents search for food hidden near explicit landmarks located within the arena.

(2) The location of the food can vary continuously. The arena does not have an internal structure providing discrete choices (as, for example, in radial mazes).

(3) The location of food is defined precisely in terms of its distance from a specific landmark (or pair of landmarks) and in a direction specified by a distal polarising cue.

(4) The location of the intra-arena landmarks can be varied across trials during acquisition. For some groups, the landmarks are in relatively fixed locations within the arena, for other groups they move around.

(5) The spatial relationships that the animals learn are necessarily allocentric as they can approach the landmarks and food from any direction.

Materials and methods

The experiments were carried out in a square open arena, 3.3 m × 3.3 m, in which rats searched for hidden food. The arena was surrounded by black ceiling-to-floor curtains on three sides and a white curtain on the remaining side, which served as a polarising cue. In experiments 2 and 3, a noise source was also placed under the white curtain as an additional polarising cue. The animals were placed into this arena at the side-walls for a series of training trials each day, one of which was nonrewarded and conducted in the absence of landmarks to increase the contingency between landmark and reward. The paths the animals took to the food were monitored by an overhead video camera connected to an on-line computerised tracking system. At the end of training, we determined what they had learned about the relative location of the food to nearby landmarks by examining the animals' search paths on transfer tests in which the food (only) had been removed. We also looked at search performance controlled by context cues in the absence of the landmarks. In experiments 1 and 2, the rats were transported to the start points in a slowly rotating opaque box, to prevent access to visual and vestibular cues (Etienne *et al.* 1986) that would enable them to establish their orientation relative to the outside world. The polarising cue rotated randomly with respect to the room between days or trials. In experiment 3, the polarising cue was kept directionally stable and the animals were not subjected to vestibular disorientation prior to the start of each trial.

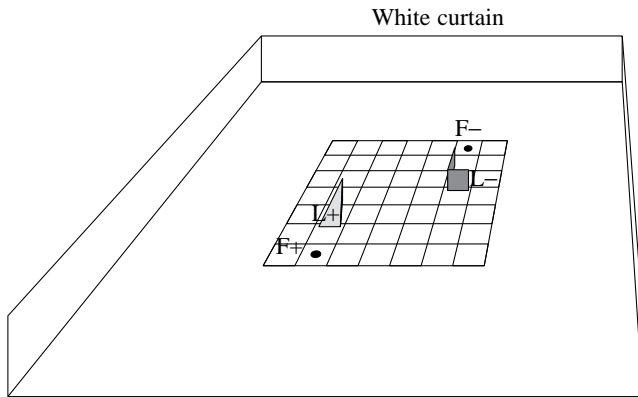


Fig. 1. Experiment 1. Diagram showing the relative positions of arena, landmarks and curtain. The landmarks (L) and food (F) locations are shown in their correct locations for group Fixed. In group Varied, the L+/F+ and L-/F- arrays were moved independently between positions in the 7×7 grid shown in the centre. The arena measures 3.3m×3.3m.

Experiment 1

Two landmarks were used in the first study (Biegler and Morris, 1993). A feeder containing accessible food (F+) was placed 40cm from one landmark (L+) opposite the white curtain (Fig. 1). Another feeder with inaccessible food (F-) was located 40cm from the second landmark (L-), in the

direction of the white curtain. There were two groups. In group ‘Varied’, these two landmark–feeder arrays were moved, from trial to trial, independently of each other and in a random sequence within a grid of 49 positions. Only the spatial relationships between each landmark and its feeder remained stable (ie. L+/F+ and L-/F-) and only the L+ landmark, together with the polarising cue, predicted the location of reward (F+). In group ‘Fixed’, both arrays remained in the same two positions throughout training. Context cues, such as the breaking of the fourfold symmetry by the white curtain and the proximity to the walls of the arena, predicted the reward location as reliably as L+. The adequacy of this design relies on subjects extracting a location-independent reference direction from the polarising cue (Taube *et al.* 1990a,b).

Both groups learned to discriminate the two landmarks, as indicated by preferential searching near L+ in tests without feeders present (Fig. 2). Other tests (data not shown) revealed that discrimination depended only on the features of L+ and L- rather than any uncontrolled cues.

However, when searching near L+, only the animals of the Fixed group focused their search at the F+ location. Those in the Varied group gave no indication of having learned anything about either distance or direction of reward from L+. A second transfer test in which the landmarks were shifted from the training location used for group Fixed indicated that L+ controlled the location of search (Fig. 2). Additional tests with

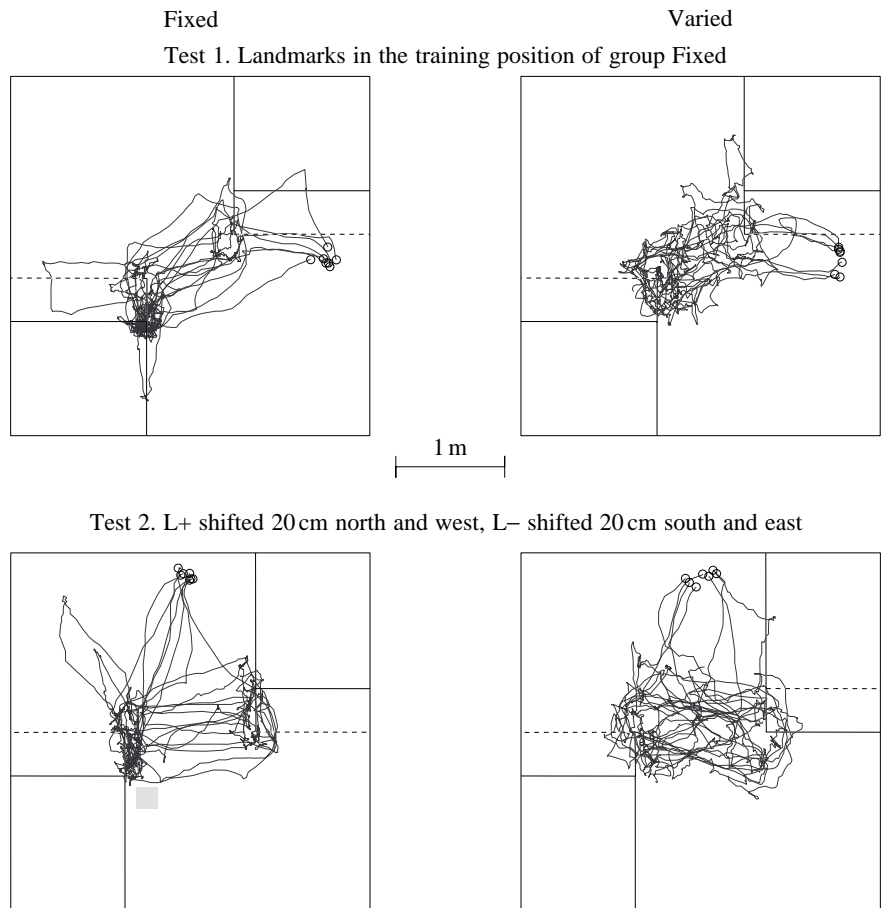


Fig. 2. Experiment 1. Superimposed paths taken by all rats in groups Fixed and Varied in test 1 (with the landmarks in the training locations of group Fixed shown in Fig. 1) and test 2 (small displacement of the landmarks). The locations of F+ and F- are marked by the meeting of two continuous lines. L+ and L- are at the intersections of broken lines. The small circles indicate the start points of search paths. The light grey square in the plot of group Fixed’s paths in test 2 shows the original location of F+ during training and in test 1. No rat searched in the training location, indicating that L+, rather than context cues, controlled the location of search. This and all subsequent diagrams have been rotated so that the polarising cues are at the top of the page, regardless of their actual orientation during tests.

landmarks removed in this and later experiments revealed that context cues alone could not account for the difference between groups Fixed and Varied.

These findings indicate that manipulation of spatial parameters can affect spatial learning without effect upon discrimination learning. This dissociation supports the view that spatial learning may be distinct from other forms of learning (O'Keefe and Nadel, 1978), but does not by itself provide any evidence that it follows different learning rules. However, we also found that a stable landmark exerted greater control over search location than a moving landmark. This result would be trivial if, in group Fixed, there was an additive effect of context cues and landmarks in directing search to the F+ location, but this was not the case. However, if context cues had no influence at all, there would be no basis for perceiving whether the landmarks were stable.

The notion of competition between cues for associative strength does not seem sufficient to account for the nature of

the interaction between context and landmarks. This is because the moving landmark would, together with the polarising cue, have been the sole spatial predictor of food while the stable landmark should have shared control with the context cues. In keeping with the argument presented in the Introduction, the finding that landmark stability aids learning seems more consistent with the idea that spatial learning involves constructing a stable map of the environment.

Unfortunately, the experiment has the weakness that the stable geometric relationship between L+ and L- in the Fixed group may have given this group directional information not available to group Varied. A further test of the principle of landmark stability was therefore required in which both groups had strictly equivalent directional information. In addition, an associative account of the advantage of having stable landmarks is possible if the subjects are taken to form a configural association (Rescorla, 1973; Sutherland and Rudy, 1989) of L+, L- and context cues as seen from each of the 49

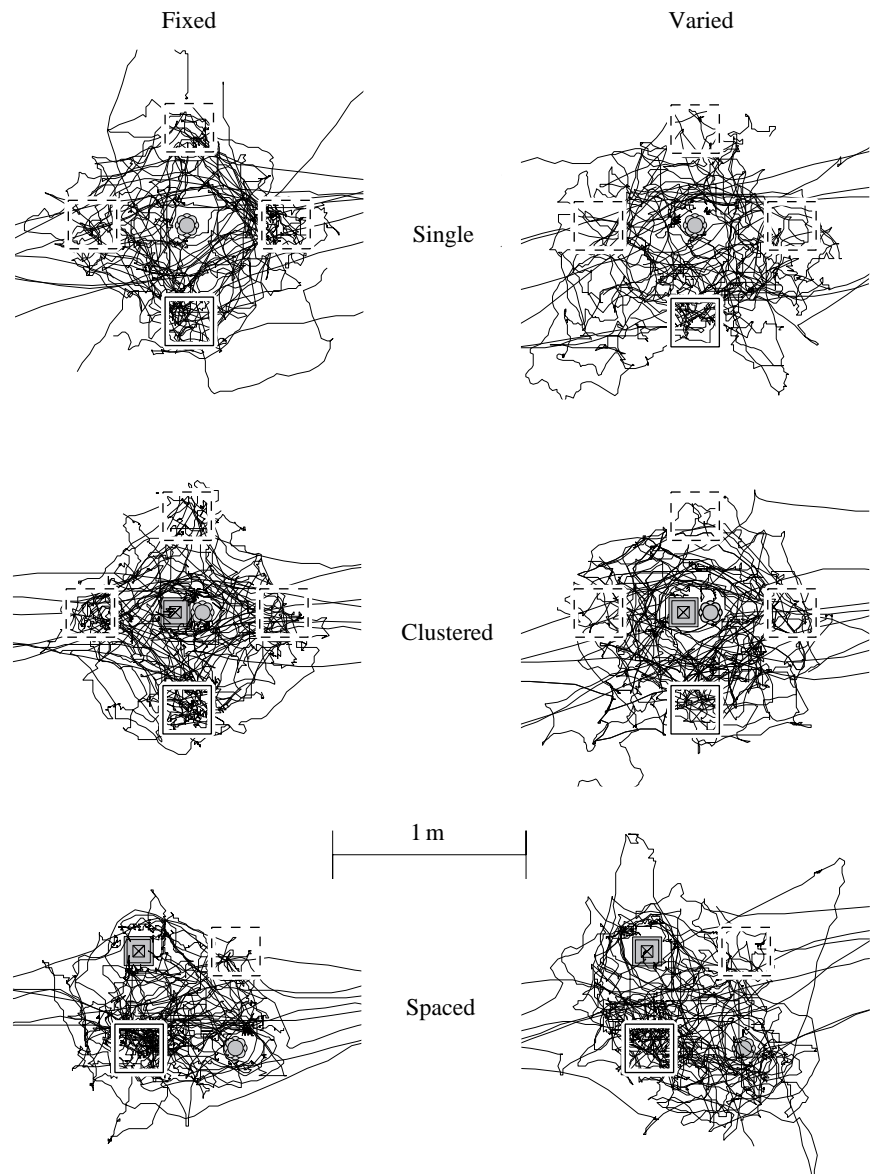


Fig. 3. Experiment 2. Paths taken during the first 30 s of test 1 (familiar location) and test 2 (novel location not used during training). Since there was no difference in the behaviour between these tests, the paths are displayed together. Only the area immediately surrounding the landmarks is shown, not the full arena as in the figures for experiment 1 above (note scale). The black squares mark the location of F+, the broken squares mark locations at an equivalent distance from the landmarks and equivalent directions to the walls of the maze. Groups Fixed-Single and Fixed-Clustered focused their search at the appropriate distance from the landmark(s) and in four discrete directions. There is a single preferred direction in groups Varied-Single and Varied-Clustered, but search is more diffuse and concentrated closer to the landmark(s).

F+ positions used in group Varied. Each of these configurations would constitute a separate task to be learned and, thus, group Varied must learn more than group Fixed. This has two implications: (1) the formation of such a configural association should be independent of the spatial arrangement of landmarks in an array, because, regardless of their arrangement, the combination of landmarks and context will be unique in each location; (2) performance should deteriorate when the animals are tested with a novel landmark location that was not experienced during training. Note that these two predictions are linked.

Experiment 2

These issues were addressed in a second experiment (R. Biegler and R. G. M. Morris, in preparation) characterised by the following main changes. (1) Fixed and Varied groups were used as before, but directional information was made equivalent in these groups by changing to radially symmetrical landmarks and by arranging for only one landmark–feeder array to be placed in the arena. (2) The landmarks within these arrays were in one of three different arrangements. In one, a ‘Single’ landmark was placed 50 cm from F+; in the second or ‘Clustered’ arrangement, two landmarks were placed side by side, 50 cm from F+; in the third or ‘Spaced’ arrangement, the same two landmarks formed a right-angled triangle with F+. (3) We examined the effects of moving the landmark–feeder arrays to novel locations in post-training transfer tests.

Taking these points in order, the overall accuracy of search

in this experiment was poorer than in experiment 1 (compare Figs 2 and 3), with only the Spaced arrangement groups showing search predominantly localised at the F+ location. This indicates that the polarising cues (white curtain and noise source; see Materials and methods) were substantially less effective than we had envisaged, raising the possibility that the apparent effect of landmark stability in experiment 1 may have been because group Fixed had access to additional directional cues. Second, however, both landmark stability and landmark arrangement did affect asymptotic performance in experiment 2. While the search distributions of the Single and Clustered arrangements were indistinguishable, there was a subtle but significant difference between groups Fixed and Varied. In the Fixed condition, search was focused at the correct distance, but in four discrete directions. In the Varied condition, the animals searched closer to the landmark(s) and had a weak preference for the correct direction. This indicates that, under conditions of equivalent directional information, translation of the landmarks around the arena across trials affects the capacity of rats to represent the distance of hidden food from a landmark. Training with the Spaced landmark arrangement led to more focused search than with the other arrangements. Group Varied–Spaced searched more accurately than group Varied–Clustered and no more poorly than group Fixed–Spaced. The comparison of the Varied–Spaced and Varied–Clustered groups indicates that placing the same two landmarks at some distance from each other improves performance, and the comparison of the Varied–Spaced with the Fixed–Spaced group indicates that,

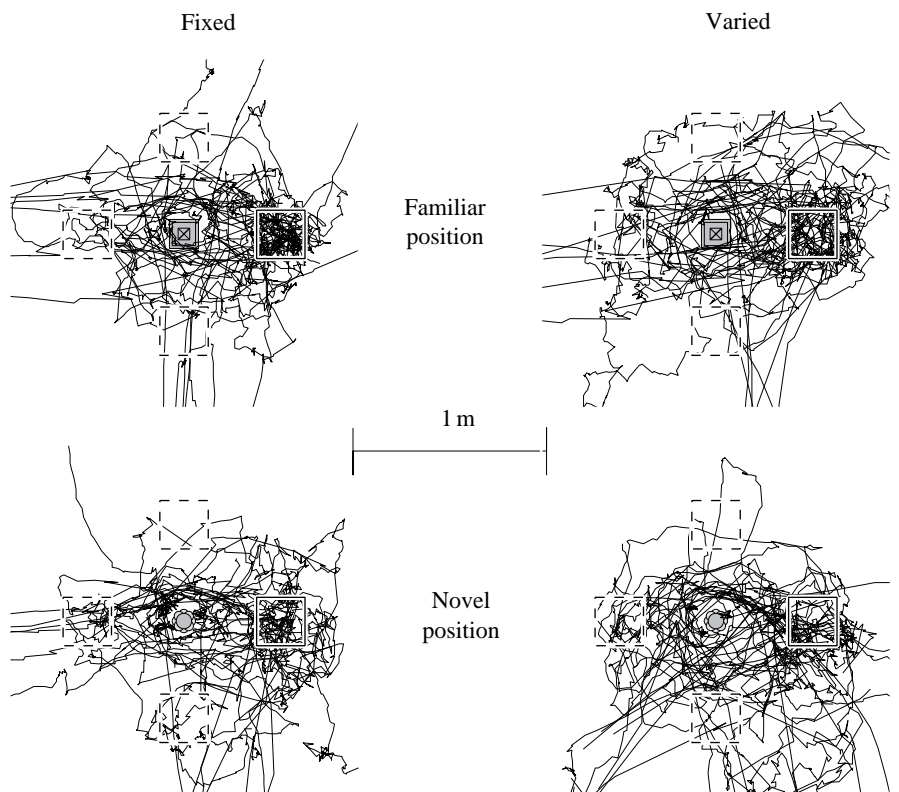


Fig. 4. Experiment 3. Paths during tests with familiar and novel landmark positions. Search was focused at the F+ location, the best performance again being that of group Fixed. For illustrative purposes, both landmarks are shown in the two tests. Although they were counterbalanced within groups, any individual rat was only trained and tested with the same landmark.

within a spaced array of two landmarks and hidden food, only local stability is required. This suggests an ability to construct small-scale maps or fragments (O'Keefe, 1991; Worden, 1992). Third, there was no difference in performance between tests with a familiar or a novel landmark location. This is consistent with cognitive mapping theory (incorporating the notion of small-scale maps or fragments), but not with the prediction we derived from the configural association theory. In addition, this theory cannot explain the better performance observed in the Spaced than in the Clustered groups. This differentiation depends on the assumption that a fragment or small map can be used independently of a larger frame of reference, while a configural association necessarily combines views of both landmark and context cue within a single 'local view'. The latter theory then gives no basis for the identification of a goal when the landmarks are moved to a novel location, except through generalisation when the novel location is sufficiently close to a familiar one. Different interpretations of both types of theory are possible, some of which are equivalent. We examine here only those interpretations which are both differentiable and appear, to us, typical of the general assumptions made.

Experiment 3

Experiment 3 replicated the training with the Single landmark arrangement of experiment 2, except for additional tests and two manipulations designed to provide more effective directional information. These manipulations were: (1) maintaining the polarising cues in a constant orientation relative to the room (see Materials and methods) throughout training and abandoning the vestibular disorientation at the start of each trial – thereby making polarising and vestibular cues mutually consistent; and (2) increasing the correlation between polarising cues and reward by removing these cues on the daily nonrewarded trial without landmarks.

Compared with experiment 2, the overall accuracy of search improved. The Fixed group focused its search in a single direction, while group Varied, although again not as good as group Fixed, was above chance in a measure of search accuracy with respect to distance (Fig. 4). However, performance declined in a novel landmark location in both groups. Thus, the combination of effective directional cues and a stable landmark location produced the best spatial learning performance, but the performance of group Varied indicates that a stable reference direction and landmark–reward distance are together sufficient to support spatial learning.

Discussion

These experiments have revealed that making one landmark the best predictor of reward location by varying its location in space, so varying the spatial relationships with reward of all other cues, decreased the control over search location exerted by that landmark. When compared with a condition in which the landmark was relatively fixed such that it and context cues

could compete for control, the better performance by group Fixed relative to group Varied was apparent in each experiment. As the contribution of the context cues could not account for the difference between the two training conditions, this finding contradicts a simple associative account.

In each of the experiments, transfer tests were conducted to explore the control over search location by context cues alone (i.e. without intramaze landmarks present). In experiment 1, no more time was spent searching in the central area of the arena than would have been expected by chance, and animals in group Fixed showed neither any focus to their search nor any increased time at the F+ location. Similar results were obtained in experiments 2 and 3. These findings indicate that, under the training conditions we used, landmark and context cues work synergistically: the intramaze landmark provided information about distance whereas the context and vestibular cues provided information with respect to direction.

The level of performance seen in experiment 2 with a single fixed landmark and ineffective directional cues was poor, but group Fixed–Single did search at an appropriate distance from the landmark. More effective directional cues in experiment 3 improved the performance of both groups and, significantly, allowed above-chance levels of performance in group Varied. In experiment 2, adding a second landmark giving redundant spatial information (Clustered arrangement) neither improved performance beyond that achieved with a single landmark nor altered the requirement for landmark stability. However, when a second landmark was placed at a distance from the first (Spaced arrangement), adding stable spatial relationships within the landmark array, performance improved yet further for both Fixed and Varied groups. Interestingly, the behaviour of group Varied–Spaced was now indistinguishable from that of group Fixed–Spaced. It appears, therefore, that increasing the number of locally stable spatial relationships aids effective representation of reward location while the mere number or salience of landmarks has no influence.

Several other studies also show an impairment of spatial learning after rearrangement of landmarks (Kraemer *et al.* 1983; Spetch and Honig, 1988; Suzuki *et al.* 1980). These studies support the notion that landmark stability is an important determinant of spatial learning, but detailed analysis is difficult because they used mazes with a rich internal structure and multiple landmarks.

Studies by Cheng (1988) and Etienne *et al.* (1990) provide evidence that the greater the size of the discrepancy between two sources of spatial information, the more weight is given to the reliability of information. If a discrepancy is small, then local cues, allowing more accurate navigation, have greater influence. If a discrepancy is large, more influence is given to distal cues and sometimes to dead reckoning.

Margules and Gallistel (1988) found that rats which ignored cues that uniquely specified a location in a rectangular environment could use a larger frame of reference to orient themselves and distinguish otherwise ambiguous locations. The often reported preference for extramaze cues (O'Keefe and Nadel, 1978; Kraemer *et al.* 1983) may reflect a strategy of

using large-scale features to distinguish locations marked by similar looking landmarks or landmark arrays. For example, the configuration of hills or the shape of a clearing is less likely to be duplicated than the presence of a bush. Any duplication of distal features that does occur is likely to be at a sufficiently large scale that dead reckoning can resolve the ambiguity.

The results of our experiments and of those discussed above are all consistent with the supposition that spatial representations are organised hierarchically, with proximal landmarks being treated as more accurate while distal features are treated as more reliable. When a conflict arises after training in a stable environment, the weight given to each source of information will depend on its *a priori* reliability and the extent of the discrepancy. Although our experiments do not distinguish between an associative and a cognitive mapping account of spatial learning, they do constrain both types of theory. For, if the results are interpreted in terms of cognitive mapping, then experiment 2 reveals that the mapping system can construct independent small-scale maps, while experiment 3 demonstrates that the information contained in such a map can be the theoretical minimum for unambiguous localisation (a distance and a direction). In contrast, if the results are interpreted in terms of associative learning theory, we have not found a spatial analogue of contingency. In three different experiments, making a single landmark the best predictor of reward location *decreased* control over search by that landmark compared with a condition where other cues could also contribute to localisation and therefore compete for control. Furthermore, spatial relationships besides mere spatial proximity (the analogue of contiguity) were shown to be determinants of learning. More than a simple association is required to account for spatial learning.

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