

Spatial Localization Does Not Require the Presence of Local Cues

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The purpose of this paper is to demonstrate that rats can rapidly learn to locate an object that they can never see, hear, or smell provided it remains in a fixed spatial location relative to distal room cues. Four groups of rats were permitted to escape from opaque water onto a platform which was either just above or just below the water surface, and in either a fixed or varied location. Learning occurred rapidly except for the group for whom the escape platform was below the water surface and moved about from place to place. Transfer tests revealed that a spatial location search strategy was employed by the group for whom the platform was below water but in a fixed location. A second experiment investigated this learning further, revealing instantaneous transfer when the rats were required to approach the platform from a novel starting position. The data of both studies are discussed in relation to recent work on spatial memory in the rat. The concept of the "acuity" of spatial memory is introduced and the procedures used may provide a new approach to comparing spatial memory with classical and instrumental conditioning.

The purpose of this paper is to describe two studies concerned with spatial localization by the rat. Crucial to the design of the experiments is the distinction between "proximal" and "distal" localization (Watson & Lashley, 1915). In "proximal" orientation, a goal object is visible (or audible, or detectable by smell) and so can be approached from a distance. Learning is straightforward as it requires no more than the operation of a motor "taxis" system (Fraenkel & Gunn, 1961) toward a significant conditional or unconditional cue. In "distal" orientation, however, the goal object is invisible, inaudible, and cannot be detected by

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smell. No "local" cues, where "local" implies cues that are spatially cooccurrent with the goal object, are available to guide the animal to the goal. Thus any "directionality" in behavior (Menzel, 1978) can only be achieved by learning about the spatial location of the goal object relative to distal cues. The present experiments provide a rigorous comparison of spatial orientation under proximal and distal conditions, matching the motor, motivational, and reinforcement parameters of the two experimental procedures.

However, while the distinction between proximal and distal orientation can be stated precisely, it is not yet clear whether it represents a valuable distinction with respect to underlying mechanisms of orientation. One problem is that few learning tasks fall neatly into one or other category. In the radial maze (Olton & Samuelson, 1976), for example, a rat will soon learn that food is only available at the ends of arms. As he moves down a chosen arm, many proximal cues guide the rat to the correct location where food may or may not be found. Only the decision about which arm to enter is made distally and, thereafter, the problem of "directionality" is rendered trivial. This is generally true of mazes which, modeled on burrow and trail systems found in nature (Barnett, 1967; Small, 1901), convert the problems of spatial localization into a series of choice-point decisions.

The present procedures abandon the necessity for choice-point decisions by forcing the spatial localization system of the animal to guide him to the exact location of the goal. One question at issue is: Can a distal localization system operate in isolation? Other related questions are: How does distal localization performance compare with proximal orientation? Is it learned as fast, or with such accurate directionality? Rats were placed into a large pool of water which also contained one of two platforms affording escape. One platform was painted black and protruded 1 cm out of the water. The rats could see this platform, swim toward it, and climb onto it. The other platform was painted silvery white and did not quite protrude out of the water. The water was rendered opaque by the addition of a small quantity of milk and consequently the underwater platform was invisible and no local cues marked its presence. Experiment 1 is a comparison of learning under the two conditions, with particular attention paid to rate of acquisition of escape behavior, speed of escape, path length, and path directionality. Various precautions were taken and control procedures introduced to ensure that the comparison between conditions was meaningful.

EXPERIMENT 1

Method

Subjects

Thirty-three male hooded rats of the Lister strain (born and bred at the Rowett Research Institute in Aberdeen) were used. They were housed in

individual cages and maintained on *ad libitum* food and water. All animals weighed between 0.4 and 0.5 Kg.

Apparatus

The apparatus consisted of a large circular pool, constructed of hardboard and lined internally with glassfiber. The dimensions of the pool were 1.30 m diameter by 0.60 m high, with the water level set at a height of 0.40 m above the base. The pool was filled and emptied via a drain system and heated to $26 \pm 1^\circ\text{C}$. The water was changed each day. The pool was placed on a metal frame support such that the water level was 0.80 m above floor level, and the entire apparatus placed in the center of a laboratory room measuring 3 by 4 m. The room had a window on one wall, a door opposite, shelves on an adjoining wall, and a cupboard opposite that. A closed-circuit videocamera with a wide-angle lens was mounted above the center of the pool and the picture relayed to recording equipment in an adjacent room.

One of the two platforms was sometimes (see below) put in the pool at particular locations. The rats could escape from the water onto the platforms. They were constructed of drain piping of 0.11 m diameter and filled with stones. There were three differences between the two platforms: (a) one was painted matt black, the other painted silvery white; (b) the black platform was 0.41 m high, 0.01 m above water level, while the other platform was 0.39 m high such that it did not protrude above the water surface; (c) when sealed at the top with glassfiber, a small dip was placed in the black platform to ensure that the rats stood in a roughly equivalent depth of water when on the visible black platform as when standing on the underwater platform (see Fig. 1). This should equate the reinforcement of escape provided by each platform.

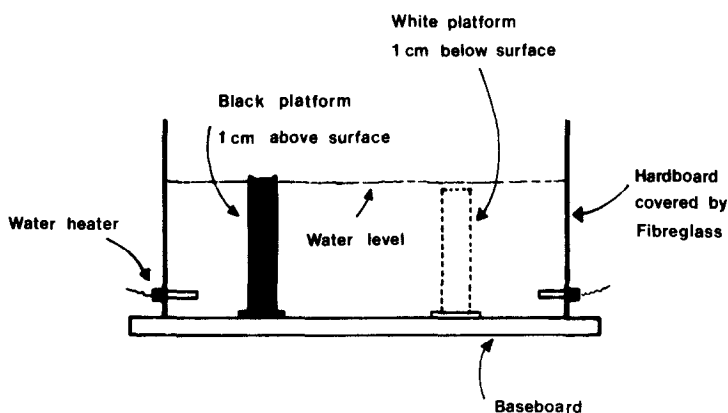


FIG. 1. A cross-sectional view of the apparatus showing both platforms in relation to the water level. Only one platform was present in any training condition. For a full description, see text.

The experimenters sat outside of the adjoining room watching the swimming of the rats except when placing a rat in the pool. An electronic timer was used to measure latencies to escape.

Procedure

The procedure followed consisted of Pretraining trials, Escape Acquisition trials, and finally Test trials.

The rats were randomly assigned to one of four groups of eight subjects. One rat was found to have difficulty in swimming during the first Pretraining session and was replaced with another animal. All data are reported from the 32 animals remaining.

Pretraining. All animals were first given 2 consecutive days in which they were placed into the pool for a period of 180 sec. The pool contained water (531 l) and 2.01 l of fresh milk (dilution ratio, 1:264), but neither platform was present. Only qualitative observations were made at this stage.

Escape Acquisition. The main training procedure began on Day 3 with all animals receiving eight escape trials as follows. Group *Cue + Place* were permitted to escape onto the black "above-water" platform which was put in a fixed location throughout training for a given animal. These locations were arbitrarily designated SW, NW, NE, and SE (not true magnetic directions) and counterbalanced across the group. A training trial began with the experimenter lowering the animal into the pool, the animal facing and close to the side wall, at position N, E, S, or W. The timer was started and the time recorded for the animal to escape from the water onto the platform. The animal remained on the platform for 60 sec before being picked up and placed into the pool again for Trial 2, this time at a different starting location. The sequence of starting locations was such that a rat started from two locations over the course of the eight training trials per day. The sequence varied from day to day. Group *Place* was treated in a similar way except that the white "underwater" platform was used, again in a fixed location. Though visible from vertically above the pool (and thus visible on the video recordings), the milk added to the water was sufficient to make the "underwater" platform very difficult to see (to the human eye) at water level. I cannot prove that the platform was *absolutely* invisible, but various procedures were adopted to assess whether any local cues coming from the platform could support learning (see below). Group *Cue-only* were trained with the black "above-water" platform, but the position of the platform in the pool was moved from trial to trial. It was only placed in position SW, NW, NE, and SE, but again in an unpredictable sequence such that it occupied two locations across the eight trials of training. Group *Place-Random* could escape onto the white "underwater" platform, but, like the previous group, this was placed in positions SW, NW, NE, and SE in an unpredictable sequence. The

purpose of this group, who could still learn that escape was possible, was to provide a behavioral check that the underwater platform offered no local cues.

Following the eight training trials given on Day 3, a further eight trials were given on Day 4. Only the sequence of start locations (for all groups) and end locations (Groups Cue-only, Place-Random) were changed. Day 5 began with a further series of four training trials by which time performance appeared to have stabilized. In addition to measuring the times to escape, videotape recordings were made of these last four training trials. The paths followed by the animal were later watched closely (in slow motion when necessary) and transcribed onto sheets depicting the pool viewed from above. The path lengths were then measured using a small map-measuring device. However, prior to doing this, the fourth training trial of Day 5 was immediately followed by one of two test procedures. The groups were subdivided, with four animals from each group doing each test. The assignment was such that, for Groups Cue+Place and Place, there was now one animal trained to each compass position in each test condition.

Test A was an assessment of the spatial bias of a trained animal. Whichever platform had been used during the preceding four trials of Day 5 was removed from the pool and the animal placed in again for a single 60-sec period. A record was taken of the movements of the animal on videotape and these were analyzed by calculating the amount of time spent in each quadrant (SW, NW, NE, and SE) of the pool.

Test B was also an assessment of spatial bias, but this time with the platform still in the pool so that the animals could learn a new spatial position. After the four training trials of Day 5, the platform was moved to a position diagonally opposite its training location (Groups Cue+Place and Place) or put in a fixed location for the first time for a sequence of four trials (Groups Cue-only and Place-Random). A record was taken both of the times to escape and the movements made by the animals. The paths followed were later transcribed and the path lengths measured as before.

In summary, rats were trained to escape from water under conditions where an escape platform was either visible or invisible, and occupied either a fixed or semirandom position within a familiar space. Both qualitative and quantitative measures of performance were taken throughout acquisition and during the course of two subsequent test procedures. A significance level of $p < 0.05$ is used throughout the paper.

Results

Pretraining

All but one of the animals could swim easily and effectively, the "poor" swimmer being replaced by another animal prior to the start of escape

acquisition. The rats adopted the characteristic adult swimming posture (Schapiro, Salas, & Vukovich, 1970) of forepaws tucked under the head and hindlegs used for forward progression. The head remained above water except for brief (<1 sec) moments. Initially, the rats were thigmotaxic, swimming around the perimeter of the pool near or against the side walls, making occasional efforts to escape by forepaw climbing movements against the side. Later they swam out into open water, crossing the pool several times during each of the initial habituation sessions of Days 1 and 2. Most animals slowed down their swimming speed as time in the water increased. Slower swimming may have been due to a lowering of core temperature, for the movements of grooming and face-washing were also slower immediately after the 180-sec exposure to the pool.

Escape Acquisition

The rats readily climbed onto the vertical platforms when they encountered them on Days 3, 4, and 5. Often the animals would then rear and/or turn around for a few seconds before making vigorous "wet-dog" shakes followed by grooming and occasional face-washing. There was no sign of the animals treating the "underwater" platform any differently from the "above-water" platform as a refuge from the water (see Fig. 2).

Acquisition of escape behavior proceeded very rapidly for three of the four groups, Group Place-Random showing considerably poorer performance than Groups Cue+Place, Place, and Cue-only (Fig. 3). The mean escape latency for Group Place was within 2 standard deviations of the terminal acquisition latency by trial 6 of acquisition. This is a very rapid absolute rate of learning by any standards but interpretation of this performance depends upon demonstration that there were no "local" cues to aid performance in this group. The first part of the statistical analysis shows that Group Place did not benefit from any local cues.

An analysis of variance by ranks of first trial escape latencies of all four groups was significant [$H(3) = 14.59$], which reflected the longer escape latencies of Groups Place and Place-Random (with the "underwater" platform) relative to Groups Cue+Place and Cue-only (with the "above-water" platform). Therefore, prior to any learning taking place, the underwater platform was *harder* to localize.

Detailed comparison of escape performance over the 20 training trials showed that there was no overlap between the mean escape latency of any animal in Group Place-Random (overall, and on Days 3, 4, and 5 considered separately) and that of any other animal in any group. Under such circumstances no formal statistical comparison seems to be necessary to claim that Group Place-Random learned the task more slowly than the other groups. It follows that the effective performance of Group Place cannot have been based on any local cues that the underwater platform may, nonetheless, offer to the rat.



FIG. 2. The rat is placed in the pool, facing the side walls; swims about the pool; and eventually finds and climbs onto the underwater platform. The animal usually stood on the platform in a half-rearing position and this was also true of the above-water platform not shown.

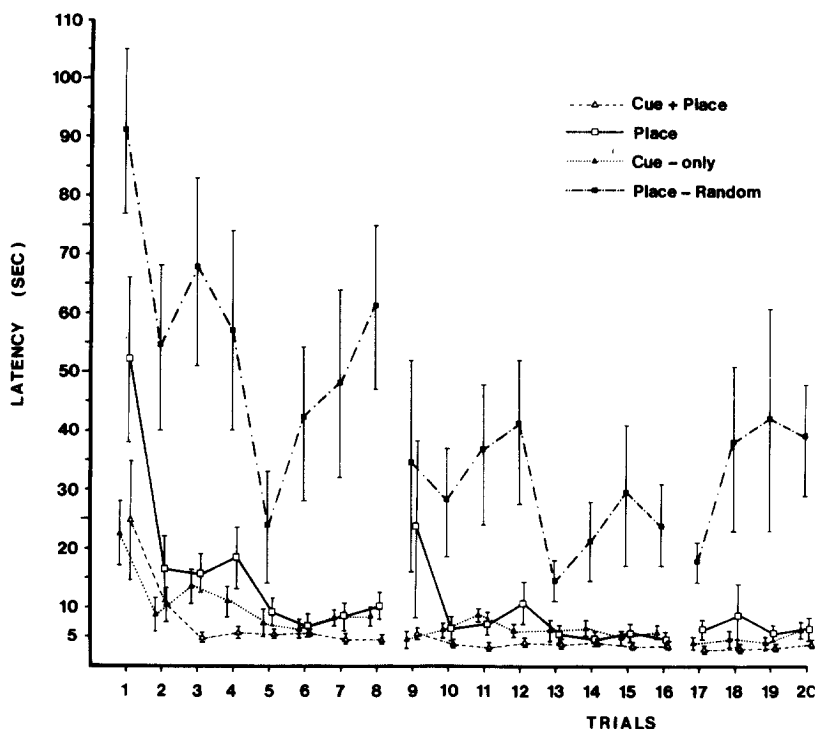


FIG. 3. Escape latency in seconds over Trials 1–20. All data points are plotted ± 1 SE

Finally, an analysis of the paths taken by the rats on the final training trial (Trial 20) showed that the rats of Group Place-Random were no more likely to head toward the platform upon placement in the pool than in any other direction. The paths were transcribed and an estimate of the direction of movement of the animal made at the arbitrary point of one radius of the pool (0.65 m) into their track. The median deviation from a heading directly toward the platform was 0° for Groups Cue+Place, Place, and Cue-only and 97.5° for Group Place-Random (range for Group Place-Random 15 to 165° ; Random performance would be 90°). A Kruskal-Wallis analysis of variance of these data was significant [$H(3) = 14.55$]. Although these data do not prove that the platform was *absolutely* invisible (inaudible, undetectable by olfaction, etc.), they do suggest that whatever local cues were available were very minimal and insufficient to support much directional learning. This is not to deny that the animals of Group Place-Random have learned something (e.g., that escape is possible), only to deny that there was any “directionality” to their behavior. It is against this poor performance that the more effective escape behavior of Group Place should be judged.

An analysis of variance of the escape latencies of Trials 1–8 of the other

three groups only was then conducted. The analysis revealed significant effects of Groups [$F(2, 21) = 9.10$] and Trials [$F(7, 147) = 12.74$] but no significant interaction [$F(14, 147) = 1.63$]. The trials effect is obvious in Fig. 3. Orthogonal comparisons between groups showed that Groups Cue+Place and Cue-only did not differ [$F(1, 21) = 1.0$] but that these two groups learned to escape slightly faster than Group Place [$F(1, 21) = 17.14$].

After performance had stabilized, it was possible to analyze the steady-state escape behavior of these same three groups (Trials 17–20). Escape latency did not vary across trials ($F < 1$), but the groups main effect was again significant [$F(2, 21) = 6.25$]. As in initial acquisition, Group Place showed longer escape latencies than the other two groups [$F(1, 21) = 11.18$] which in turn did not differ [$F(1, 21) = 1.32$].

An analysis of the path lengths of the transcribed Trials 17–20 was then conducted. Group Place-Random had very long mean path lengths and considerable trial-to-trial variability. As before in the latency data, there was no overlap in the scores of this group and the mean path lengths of any animal in the other three groups (Fig. 4). Analysis was therefore restricted again to Groups Cue+Place, Place, and Cue-only, revealing a

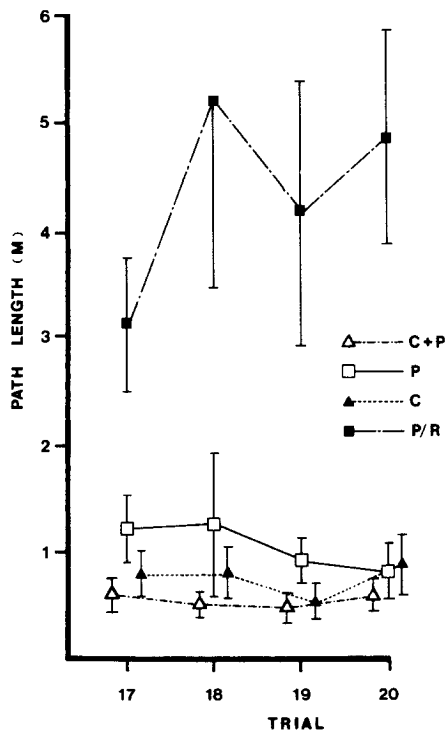


FIG. 4. Path lengths in meters over Trials 17–20 (± 1 SE).

main effect of Groups [$F(2, 21) = 5.88$] and path length stability across trials ($F < 1$).

Subsequent orthogonal tests showed that the two Cue groups took shorter paths to the platform [$F(1, 21) = 9.92$], and that their path lengths did not differ [$F(1, 21) = 1.84$].

Data have already been presented above indicating that the three groups which learned the task well were all showing excellent "directionality" in their paths toward the escape platform, and from all four starting locations of N, S, E, and W. Figure 5 shows the tracks taken over Trials 17 through 20 of the animal in each group just worse than the median (there are an even number of animals in each group). The animals were free to move off in any direction in the pool upon release; they were not required to head for the platform. However, only the rats in Group Place-Random behaved in a nondirectional manner.

Test Trial Performance

Qualitative observations. Figure 6 shows the paths taken during the first test trial by the same four animals whose paths were shown in Fig. 5.

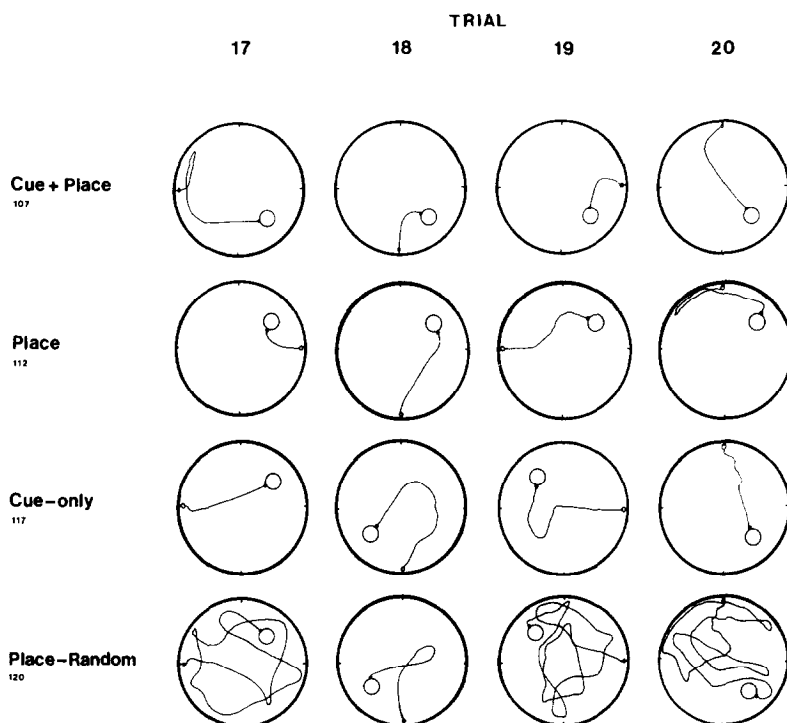


FIG. 5. A vertical view of the tracks taken by the rat in each group just poorer than the median (with respect to directionality). The paths are reasonably direct for Rats 107, 112, and 117, while Rat 120 of Group Place-Random swims all over the pool. Platform size is drawn larger than to scale for purposes of clarity.

Rat 107 of Group Cue+Place shows a slight directional bias toward the SE quadrant when tested with the platform absent, while Rat 112 of Group Place shows a much stronger spatial bias toward the NE quadrant which had been his goal platform's position throughout training. For this first time, the platform is now in the SW quadrant and, although rapid escape from the water is possible for the animal, he shows the novel behavioral strategy of searching for the hidden platform in the quadrant where it used to be located. The animal was, of course, *never* trained nor observed to search in this specific way but the behavior nonetheless emerges "spontaneously." Rat 117 of Group Cue-only is used to looking for the above water platform in a variety of locations about the pool and finds it easily and directly. Rat 120 of Group Place-Random, tested without the platform, adopts a semisystematic search strategy until he is removed after 60 sec. This qualitative picture is supplemented by formal quantitative analysis of Test A and Test B.

Test A. The performance of the four animals in each subgroup on Test A (without platform) is shown in Fig. 7. Group Place animals show a strong directional bias toward their respective training quadrant. The effect is present but considerably weaker in Group Cue+Place. Third, there appear to be no directional biases-induced nonspecifically by escape training as indicated in the performance of Groups Place-Random and Cue-only. An analysis of variance was conducted of the time spent in each of the four quadrants (SW, NW, NE, and SE) by each of the four Groups. A significant Groups \times Quadrants interaction [$F(6, 36) = 3.59$] was obtained, even when the interaction term degrees of freedom were reduced, in accord with the fact that each rat's scores for the four quadrants summed to 60 sec. subsequent tests revealed that the time spent in the training quadrant by Group Place was greater than the time spent in the same quadrant by Group Cue+Place [$F(1, 36) = 5.85$], but that the time spent in the training quadrant by Group Cue+Place did not depart from the null hypothesis value of 15 sec [$F(1, 36) = 4.05$]. The path lengths of Test A were not measured.

Test B. The performance of the four animals in each subgroup on Test B is shown in Figs. 8A and B. As in Test A, the rats in Group Place swam to

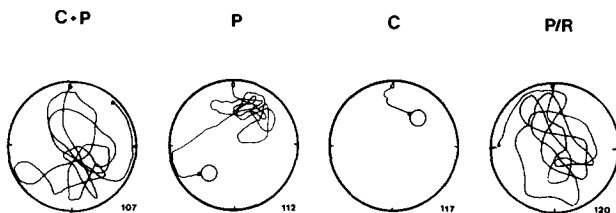


FIG. 6. A vertical view of the tracks taken by the same animals as in Fig. 5 on their first test trial. For Rats 107 and 120, it was Test B; for Rats 112 and 117, it was Test A. See text for a detailed discussion. Platform size not to scale.

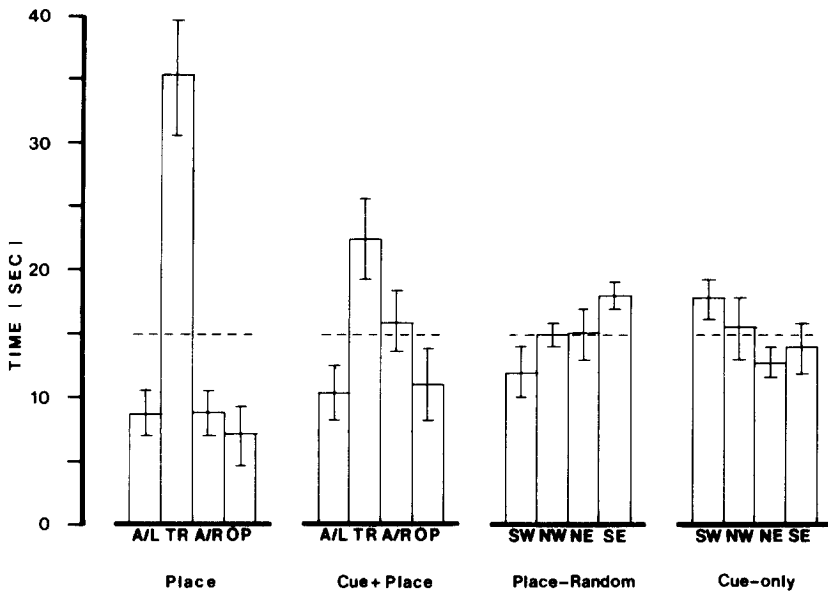


FIG. 7. The duration of time (sec) spent in each quadrant in Test A (± 1 SE). TR is the training quadrant, A/L and A/R are the adjacent quadrants to the left and to the right, respectively, and OP is the opposite quadrant (Groups Place and Cue+Place). The other groups' data are organized with respect to compass positions. Only Group Place shows a strong spatial bias.

and about the place where the platform used to be located until eventually, and probably by chance, they swam into the platform in its new location. Learning about the new location of the platform then proceeded very rapidly. Some place-bound swimming was also observed in Group Cue+Place despite the fact that the platform was visibly in a new location. The performance of the other two groups is of interest because this test condition is their first experience with the platform placed in a fixed location for a series of four trials. Group Place-Random, in particular, shows a marked decrease in response latency across the four trials and no obvious sign that it has learned to ignore place cues.

Formal analysis of escape latency indicated significant Groups [$F(3, 12) = 12.89$] and Trials [$F(3, 36) = 3.78$] effects but no significant interaction. Subsequent orthogonal comparisons indicated that Group Place escaped to the new platform location significantly slower than Group Place-Random [$F(1, 12) = 18.84$], a finding which reflects the place bound swimming of Group Place animals, particularly on the first test trial. Group Cue+Place was not significantly slower to escape than Group Cue-only [$F(1, 12) = 3.49$] though the effect approached significance. Analysis of path lengths over this series of test trials indicated an identical pattern and the similarity of Figs. 8A and B should be noted.

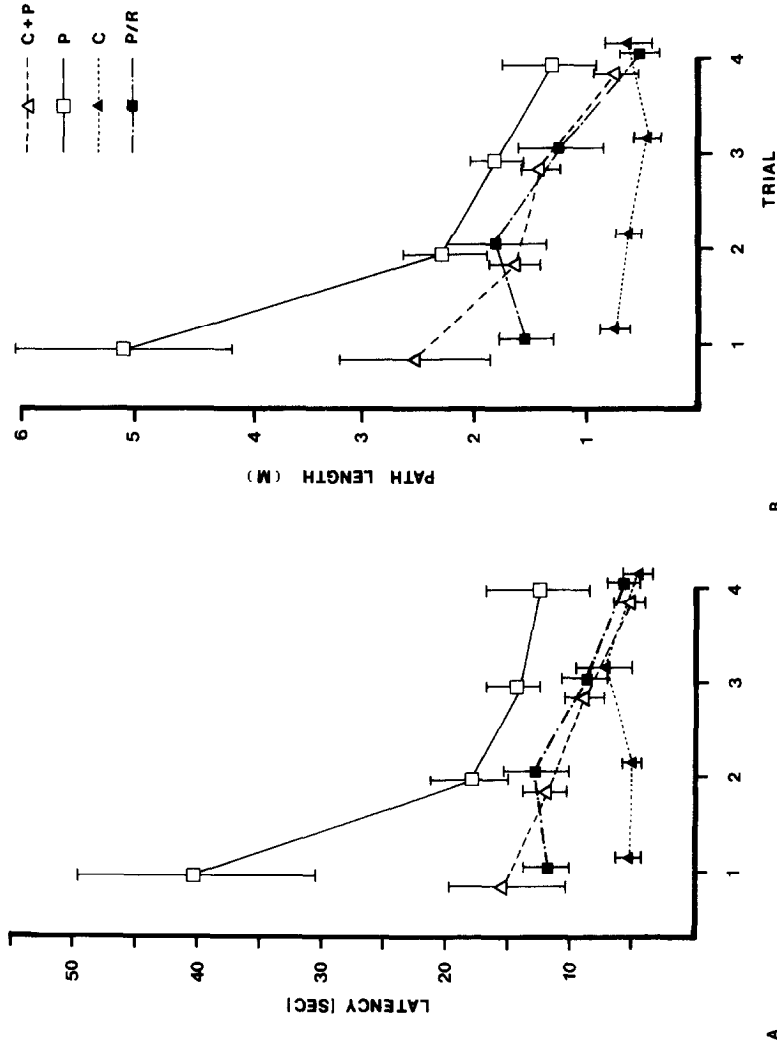


FIG. 8. The escape latency (sec) and path length (m) over Trials 1-4 of Test B (± 1 SE). Group Place animals searched where the platform used to be located on the first test trial and then rapidly learned to approach the new platform location by a slower route.

Discussion

The results show that rats learn to find an object that they cannot see, hear, or smell, by locating its position in a familiar space. When allowed to approach it from any direction, they show good "directionality" in the paths taken. Although performance does not quite match that shown when the goal object is visible, localization is nevertheless learned very rapidly; the rats come within 2 standard deviations of their terminal acquisition performance by Trial 6 of training. The effective performance of Group Place, both in absolute terms and relative to Group Place-Random, implies that distal localization can operate in isolation. This answers one question raised in the introduction to this paper.

Several detailed aspects of the results are of interest. One is the terminal acquisition performance of the three groups that did learn the task well, which shows that the groups with the "above-water" platform took significantly shorter paths and escaped quicker than Group Place. This indicates that, although distal cues are sufficient to get the animals to the correct general location of the platform, proximal cues do improve performance. However, the sudden emergence during the test trials of a spatial-location search strategy indicates that Group Place have learned a lot about the spatial location of the hidden platform. Having swum to the correct general area and now been unable to locate the platform, the rats searched systematically in the vicinity until later swimming off elsewhere. The performance of Group Place-Random is a third point of interest in the data. These animals showed no directionality in their platform approach paths but this does not imply that they learned nothing, as their escape latencies did drop over training, stabilizing at about 30 sec. This group may have learned (1) that "escape was possible" and (2) that the platform providing escape was not beside the side walls of the pool. Accordingly, it is hard to assess the significance of their rapid acquisition of fast escape latencies during Test B. Had the animals learned to "tune out" place cues (Moore, 1979), a crossover in the escape latencies of Group Place and Place-Random might have been predicted. This did not occur, but in the absence of appropriate control groups the apparent lack of any retardation effect cannot be assessed. What Group Place-Random does establish is that the very effective performance of Group Place cannot have been due to any olfactory or other local cues associated with the platform. The experiment does, therefore, seem to have been successful in demonstrating localization of a hidden object. How did the rats do this?

One theory is that the animals formed a "spatial map" (O'Keefe & Nadel, 1978) of the environment representing the relative locations of "extramaze" cues and the position of the platform. When placed in the pool, the rats first established their own location with reference to the map. Some processing system, whose *modus operandi* has never been

explained, then gives rise to appropriate directional movements toward the known location of the invisible platform. This explanation is primarily about the *form* in which knowledge about the environment is stored in memory (see Nadel & Willner, 1980), and carries with it the corollary that referring to the environment in an experiment such as this as a "background cue" is unhelpful. A particular feature of an explanation in terms of spatial mapping is the notion that such forms of representation permit behavioral flexibility, provided the environment remains constant. Moving the platform to the opposite quadrant (as in Test B) should not affect the representation of space outside the pool and localization behavior should, as it did, adapt to the new escape location very rapidly. This is important because it is tempting to think of Test B as a kind of "spatial reversal" task but such a description is misleading because none of the spatial relationships or associations encoded within the map need to be changed; only the "map entry" denoting the position of the platform is changed.

As an alternative to the "spatial mapping" theory, how might associative mechanisms, such as those responsible for S-R or S-S conditioning (Mackintosh, 1975), account for the performance of Group Place? An associative account would presumably deny that the rats are learning the location of the platform or even about the relative positions of distinct extramaze cues. With rules only governing the associability of elements separated in time (but see Rescorla, 1978), an S-S account would be forced to argue that the rats may be learning four distinct cue-approach responses. Deutsch's (1960) theory must offer an identical account. Placed in position N, the rats receive a pattern of exogeneous stimulation distinct from that at S, E, or W. In the presence of such cues, approach toward some discriminable distal cue (Restle, 1957) takes in the platform along the path and so allows escape from the water. An S-R account might be that the rat learns to swim off at various angles from the side walls from the different starting positions (Potegal, 1968). These explanations are not without their difficulties: for example, why did the animals of Group Place search around the location where the platform used to be located on the first test trial of both Tests A and B? Such behavior had never been explicitly trained and because of the accuracy of localization in Group Place was in fact rarely observed during training.

Experiment 2 is an attempt to resolve the matter through the use of a transfer test in which the animal is required to approach the platform from a novel start location on a test trial. The "spatial map" hypothesis predicts no disruption of learned performance whereas the S-R and S-S conditioning hypotheses do predict disruption. The experiment is designed to maximize the opportunity for learning a specific cue-approach response by giving training from a single start location to all animals. Different groups are then given different transfer tests to provide a rigorous test of true location learning.

EXPERIMENT 2

Method

Subjects

Fifteen male hooded rats of the Lister strain were used. They were similar in every respect to those used in Experiment 1.

Apparatus

The same swimming pool was used, with training and testing conducted at the same water temperature of $26 \pm 1^\circ\text{C}$. Only the silvery white underwater platform was used in this experiment.

Procedure

The procedure followed consisted of Pretraining trial, Escape Acquisition trials, and finally Test trials.

Pretraining. On Day 1, all animals were placed in the pool without a platform to swim for 180 sec.

Training. All animals were given 15 escape trials, over 3 days (six trials on Days 2 and 3, and three trials on Day 4), with *every* trial started at the arbitrarily designated W position and the platform always in position NE. The groups differed only with respect to what happened in the Test trials, which followed immediately after the 15th training trial.

Test trials. There were three successive test trials for all animals. Group *Same-Place* ($N = 6$) was given test trials with the platform still in position NE, but with the animals started successively from three novel start locations N, S, and E. The sequences of start location were counterbalanced across animals within the group. Each animal of Group *New-Place* ($N = 6$) was required to escape to the platform using the same sequences of novel start locations but the platform was moved on each test trial. The position of the platform was SE when N was the start location; SW when E; and NW when S was the start location. Thus pairs of "platform position" and "start location" during testing correspond to the angular relationship held constant throughout training. If the rats were learning to swim away from the side walls at a particular angle, this series of test trials should present no difficulty. Finally, Group *Control* ($N = 3$) was given three further trials from W to the platform in NE to provide a stable, between subjects measure of the baseline escape latency against which to assess the test session performance of the other two groups.

Results

Escape performance stabilized by Day 4, with all animals showing latencies on Trials 12–15 comparable to those of Group Place animals in Experiment 1; performance was not radically better despite starting each training trial from the same location.

The test trial performance is shown in Fig. 9A. No animal in Group New-Place showed a mean escape latency over the test trials that was faster than any animal in Groups Same-Place and Control. As there is evidently considerable test session heterogeneity of variance, formal statistical analysis would have to be nonparametric and this does not seem to be necessary. The scores of Groups Same-Place and Control overlap considerably. When the same data are replotted as a function of the starting location on the test trials without regard to the order for any given animal (Fig. 9B), this simple picture remains unchanged. In particular, there is no sign that escape latencies are any different in Group Same-Place when the animals have to swim southeasterly from an N starting location, northwesterly from E, or north-northeasterly from S. In short, escape performance is *invariant* to starting position.

Figure 10 shows the tracks taken on the first test trial by each animal in each group; these tracks confirm the quantitative data and indicate that the rats have learned where the platform is located: rats in Group Same-Place move toward the platform from three novel start locations, and those of Group New-Place search first in the old platform position of NE.

Discussion

The results of this experiment offer clear evidence for true-location learning in the rat. The animals of Group Same-Place were able to adapt to finding the platform from three novel locations successively with no measurable increase in latency. Since completion of this experiment, Olton (1979) has also drawn attention to the distinction that can be drawn between a "direction" strategy and a "location" strategy. The present results certainly support this distinction. In particular, no evidence was obtained of the rats learning either of two possible "directional" strategies. They did not form the S-R association of swimming off at a particular angle from the side walls, as indicated by the poor performance of Group New-Place; nor had they acquired any simple S-S association of swimming toward a specific distal cue (Restle, 1957) as indicated by the lack of any effect of starting location upon latency in Group Same-Place. One might wish to salvage the S-S account by referring to the distal room cues as a single "background cue" which the animal approaches. To do this, one has to argue that the same set of actual physical room cues give rise to a constellation of "internal" background cues depending on the position of the rat in the room. On the face of it, this is reasonable as the room surely looks, smells, and/or sounds different at different positions. However, how does the animal structure this knowledge? How does he learn the geographical relationship between one internal "background cue" and another? Moreover, under the transfer conditions of the present experiment, how is he able to approach the "background cue" that served as the goal in training from a novel starting position from which the room

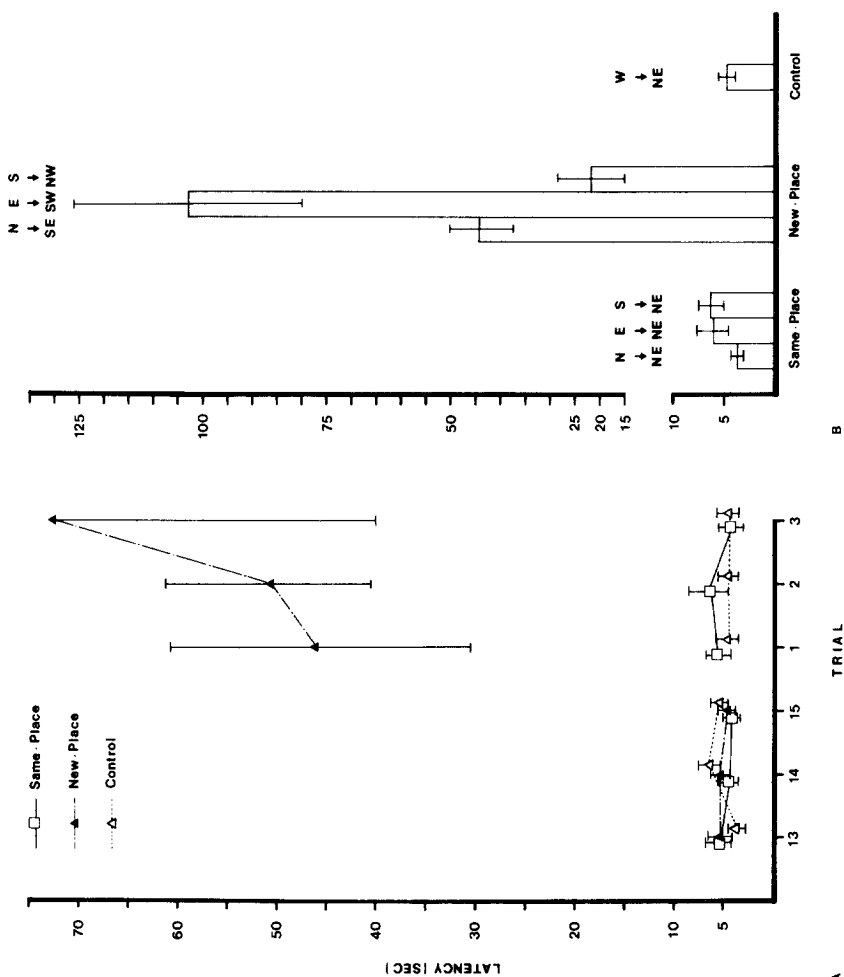


FIG. 9. The escape latency (sec) over Trials 12-15 of training in Experiment 2 and the test Trials 1-3 (± 1 SE). The test trial data only are plotted in a different way in (b). The scores have been combined, not by order of test trial, but by which starting and end location was used on that trial. Thus, the worst performance was in Group New-Place when required to swim from E to SW.

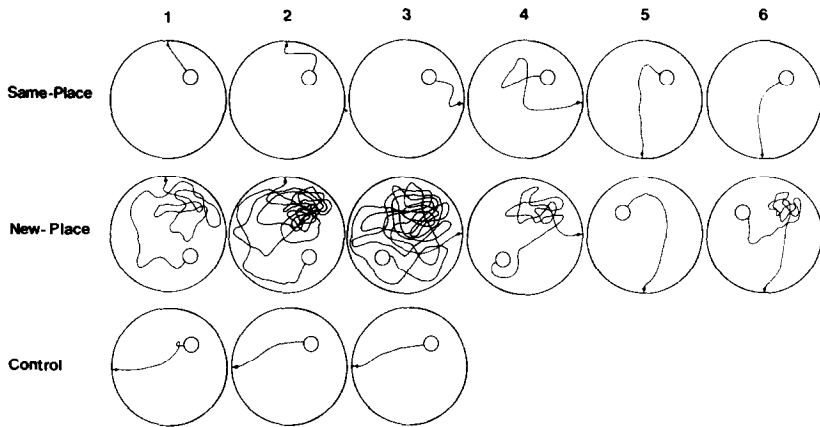


FIG. 10. A vertical view of the tracks taken by all animals in the experiment on the first test trial. Note the persistent searching in the old location by five of the six animals in Group New-Place; and instantaneous transfer to new path directions (relative to the control group) in Group Same-Place. Platform size not to scale.

presumably looks, sounds, and smells different. The cognitive mapping account (O'Keefe & Nadel, 1978) is the most parsimonious interpretation of the data with its explicit claim that the stored representation of the distal room cues permits the generation of novel directional behavior.

GENERAL DISCUSSION

The most important finding of this study is the demonstration that rats can rapidly learn to approach a spatially fixed object that they can never see, hear, or smell. This finding implies that it may be useful to consider what may be called the "acuity" of spatial memory. Spatial mapping, as a system of representing knowledge about the environment, makes it possible to distinguish one location in a familiar environment from another. The acuity of the system, as shown in behavior, would be a joint product of the processing limitations of the system in a given species and the discriminability of the objects in the environment (Roberts, 1979). In the uncontrolled environment used in these studies, laboratory rats accurately approached a hidden platform occupying 1/140th the surface area of the pool; and confined their initial efforts at searching for it (when it had been removed) to the immediately adjacent area. In a rough absolute sense, this indicates that whatever system the rats used was quite efficient and capable of processing sensory information from distal cues at least 2 m away. It is generally believed that cue-response and cue-reinforcement separation results in severe deficits in discrimination learning (Cowey, 1968). For example, Milner, Goodale, and Morton (1979) report that separation of as little as 6 cm between visual discriminanda and response location *totally* disrupts discriminative performance in rats. In the present

experiments, rats clearly discriminated spatial locations within the pool solely with respect to distal cues, and aspects of their behavior on transfer tests show that they were not directly "approaching" specific distal cues. Such a level of performance was realized despite the cues being nearly two orders of magnitude further away than in the study of Milner *et al.* (1979). Learning the task also proceeded extremely rapidly compared to visual discrimination performance, which rarely takes less than 100 trials (Sutherland & Mackintosh, 1971). It is difficult to escape the conclusion that spatial localization is a specialized skill.

However, this interpretation needs to be considered more thoroughly. The second question posed at the outset of this paper was as follows: Are the mechanisms underlying spatial mapping different from those responsible for instrumental and classical conditioning? One relevant claim that has been made about spatial mapping is that it permits "behavioural flexibility" (O'Keefe & Nadel, 1978). There were three separate demonstrations of this putative flexibility in these studies: (1) the sudden emergence of a search strategy never seen in training when the hidden platform was moved or removed (Experiments 1 and 2); (2) the speed with which the rats learned a new platform location (Experiment 1); and (3) the ability of the rats to show instantaneous transfer of rapid escape latencies to new starting locations coupled with no evidence that the direction of approach to the platform in any way influenced accuracy or latency (Experiment 2). How should these observations be assessed? Certainly, they support the "cognitive mapping" theory (O'Keefe & Nadel, 1978) of spatial localization. However, they are only weak evidence for the argument that spatial mapping relies on distinct associative mechanisms from those involved in other forms of conditioning. Very sudden changes in instrumentally conditioned behavior are seen during classical conditioning, as in the conditioned emotional response (Estes & Skinner, 1943); and instantaneous transfer of control occurs when a stimulus, conditioned off the baseline, is presented to an animal permitted to perform an instrumental response (Rescorla & Solomon, 1967; Trapold & Overmier, 1972). This leaves only the claim about the speed with which the rats learned a new spatial location, an observation that has not been thoroughly studied in these experiments and constitutes at best very weak grounds for arguing that the flexibility of spatial mapping is in any sense distinctive. The problem of assessing the supposed flexibility of spatial mapping is aggravated by the fact that it is still not clear how knowledge is translated into action. Neither O'Keefe and Nadel (1978) nor Nadel and Willner (1980) outline the mechanisms by which directional movements are selected and sequenced to move an animal from place A to place B.

Inspired in part by consideration of the biological function of spatial memory [e.g. foraging, Kamil (1978)], the present techniques may prove useful to those interested in brain mechanisms responsible for spatial

orientation and working memory (O'Keefe, Nadal, Keightly, & Kill, 1975; Olton, Becker, & Handleman, 1979). The results provide support for the cognitive mapping theory of spatial localization but no definite evidence that the processes underlying the formation of a map or its use in behavior are distinct from those processes explored in traditional studies of associative learning. However, systematic comparisons may be possible using procedures known to reveal phenomena characteristic of instrumental and/or classical conditioning. Examples are latent inhibition and blocking, both of which are easily investigated in this task precisely because the rats are not required to learn a list of locations.

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