ECHOLOCATION IN RATS

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Do rats use the echoes of sounds they produce to localize objects? In a preliminary report (8) we presented evidence that blinded rats can localize and avoid barriers in this way. Several tests indicated that the performance was based on auditory cues. For example, occluding the animals' ears by taping down the pinnas impaired discrimination of the position of the barriers. It was tempting to believe that the auditory cues might be echoes of the ultrasonic cries that the rat has been shown to make (1). However, monitoring the performance with a condenser microphone showed that the ultrasonic cries were given very rarely in the maze, and the cries did not seem to be related to the discrimination. The sum of the evidence suggested that rats, like human beings, can use the echoes of incidental, nonvocal sounds they produce to detect objects in their environment.

We have conducted further experiments on this subject for two purposes: (*a*) To test more thoroughly whether the discrimination in our test situation is indeed based on auditory cues. (*b*) If it is based on auditory cues, to test whether these cues are sounds produced by the animal rather than sounds coming from other sources in the environment. For the first purpose, we tested the performance of animals before and after impairing their hearing. For the second purpose, we selected several experimental situations by means of a "model rat" that had a loudspeaker as its sound source and a microphone as its auditory receptor. This device allowed us to determine whether or not an echolocation cue was available from each type of test situation employed. To the extent that the real rats' performance could be predicted from the model rat's "discrimination," the hypothesis of echolocation would be supported.

METHOD

The test apparatus was an elevated maze whose floor plan is shown in Fig. 1. During pretraining, *S* was fed its daily ration on the goal platform for four days. Then a diagonal path was placed between the start and the goal platform, and *S* was run from start to goal 4 trials a day for five days. Paths *L* and *R* were not available to *S* during pretraining. After the nine days of pretraining, the diagonal was removed, and paths *L* and *R* were made available. On each trial, either path *L* or path *R* was blocked 20 cm. from its beginning by a vertical, sheet-metal barrier, *B*, which measured 15 by 15 cm. The barriers were suspended independently of the maze, as shown in Fig. 2, thus excluding differential vibratory-tactile cues on the two paths. Each path was blocked on half the trials in each series of 10 trials. Five trials were given on the first day, 5 on the second, and 10 on the third, fourth, and fifth. Thereafter, 20 trials were run per day, and 14 different sequences of blocked alleys were used in irregular order. A response was counted incorrect if *S* placed all four feet on the blocked alley; when a rat progressed this far, contact with the barrier was likely. When *S* reached the goal platform, it was confined there by guillotine doors, *G*, for a short feeding period while its performance was recorded and the barriers were set for the next trial. The orientation of the maze in the room was changed each day in an attempt to avoid any constant extra-maze cues.

The standard situation of barriers, perpendicular to the direction of the paths, and the other maze conditions were tested with the loudspeaker-microphone model of the rat. A small speaker and microphone were placed close together at the choice point, and they were directed alternately at the open and blocked alleys. When the barriers were in the standard position as at *B* in Fig. 1 and as shown in Fig. 2, the model could "discriminate"; i.e., a greater intensity of sound was picked up by the microphone when it and the speaker were directed at the blocked alley than when they were directed at the open alley. An animal that could echolocate might then be expected to discriminate the open from the blocked alley in this situation.

When the angle of the barriers with respect to the pathways was changed from 90° to 45°, as shown by the lines labeled 45° in Fig. 1, the model could no longer discriminate. In the 45° case, the barrier did not reflect sound back to the choice point but, rather, out to the side of the maze. Another condition in which the model could not discriminate was obtained by making the barriers out of hardware cloth with a ½-in. mesh. Such a barrier, even at 90°, could reflect almost none of the sound back to the choice point. Echolocation would be of little help in these two situations.

Finally, a condition was found in which the discrimination was reversed for the model. When the barriers were set at 135°, the opened barrier faced the choice point perpendicularly, as shown by the dashed line labeled "135° open" in Fig. 1. Thus, the opened barrier reflected back to the choice point some of the sound that originated at the choice point. The closed barrier, on the other hand, reflected sound from the choice point out across the center of the maze. While

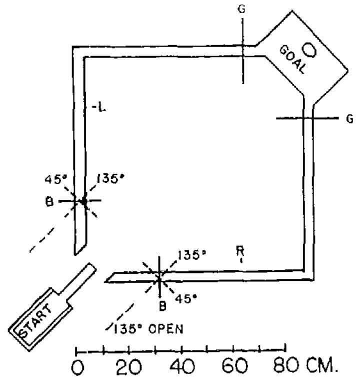

FIG. 1. Floor plan of the elevated maze used in the experiment.

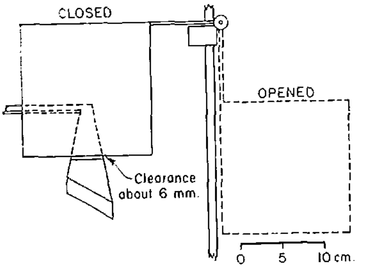

FIG. 2. View of barrier from choice point. Standard condition.

the open and blocked alleys could be discriminated, the cues were weaker than in the 90° condition, and they were reversed in direction.

In the main experiment, five rats were put through the procedures described above. The results of this experiment will be described in detail. Two other groups of animals were tested with some of these procedures; their results will be mentioned in relation to those of the main experiment.

As *a final experimental procedure in the main experiment* and in one of the other experiments, the eardrums of the animals were punctured with a probe, and the ossicles were displaced, thus permanently impairing hearing.

The *Ss* in all experiments were pigmented female rats from the Department of Psychology colony. They were enucleated just before the start of pretraining. Ages ranged from 70 to 85 days at the beginning of pretraining.

RESULTS

The results of the main experiment are presented in Fig 3. Each point represents both the number and the percentage of correct choices made by the five *Ss* in each block of 20 trials.

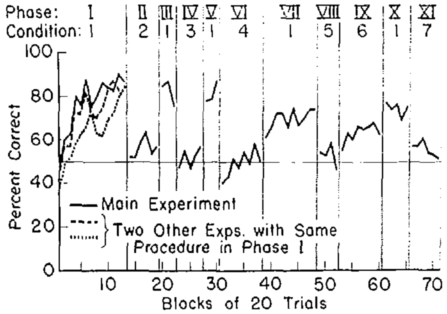

FIG. 3. Per cent correct choices on each block of 20 trials in the main experiment. In Phase I only, comparable data from two other experiments.

Phase	Condition
I, III, V, VII, X	1. Standard barriers 90° to path.
II	2. Standard barriers 45° to path.
IV	3. Hardware-cloth barriers 90° to path.
VI	4. Standard barriers 135° to path.
VIII	5. Sound-producing barriers; sound weak.
IX	6. Sound-producing barriers; sound strong.
XI	7. Standard barriers 90° to path; rats partially deafened.

Phase I, original learning. During the original learning, the barriers were in the 90° position. The closed barrier would thus reflect sound produced at the choice point back in the direction of the choice point and would provide a cue for echolocation. The solid line represents the performance of the five animals in this experiment. (A sixth rat was discarded when it showed no signs of learning after 260 trials.) The dashed and dotted lines represent the performance of two other groups of animals ($n = 3$ and $n = 6$, respectively) that received the same original training in other experiments. That the animals learned to avoid the barriers is demonstrated by calculation of the significance of the difference between the successes on the first and last blocks of trials in the original learning. On block 1, the mean per cent correct was 43.04. On block 12, the last on which all animals are represented, it was 84.29. The difference is significant ($\sigma_{\bar{x}} = 3.38$; $t = 12.20$; $p < .01$, $df = 13$). Not only was performance in the last block of trials significantly above 50 per cent, but that in the first block was significantly below 50 per cent. This suggests that the rats were discriminating from the start, but that their original tendency was to approach and inspect the barrier. According to this interpretation, the rats had to learn to *avoid* the barrier, but they did not have to learn to *detect* it. Following this interpretation, we later built a maze in which the rat approached a barrier and found food behind it. While there was some tendency for animals to discriminate from the start in this maze, performance remained mediocre, perhaps because of other undesirable features.

Phase II, barriers at 45°. Under this condition, sound produced at the choice point would be reflected by the closed barrier out to the side of the maze, furnishing no cue for echolocation. During the six days in which this condition was used, performance averaged 56.31 per cent correct. This is significantly lower than performance at the end of original training ($\sigma\bar{x} = 4.82$; $t = 6.38$, 4 df; $p < .01$). At the same time, the level of discrimination in Phase II remained significantly better than the chance level of 50 per cent ($\sigma\bar{x} = 1.60$; $t = 3.94$; $p < .02$), indicating that there was still some discriminable cue in the situation. At the door of the starting box, S faced the barrier almost perpendicularly, and it is possible that it could receive some echolocation cues here.

Phase III, barriers at 90°. When the barriers were returned to 90°, the performance recovered at once. It averaged 82.34 per cent correct during the 60 trials of this phase. This performance was significantly superior to that in Phase II ($\sigma\bar{x} = 2.86$; $t = 9.11$; $p < .01$).

Phase IV, hardware-cloth barriers. When hardware-cloth barriers were substituted for the sheet-metal barriers, the model rat indicated that there was no cue for echolocation. The performance of the live rats dropped to a mean of 51.80 per cent during the 100 trials under this condition. The drop from the mean performance of Phase III was significant ($\sigma\bar{x} = 2.92$; $t = 10.44$; $p < .01$). In this case, the level of performance was not significantly greater than 50 per cent ($\sigma\bar{x} = 1.75$; $t = 1.03$).

Phase V, barriers at 90°. When the sheet-metal barriers were used again, the percentage of correct responses returned to a mean of 81.33 during the 60 trials of this phase. The improvement over Phase IV was significant ($\sigma\bar{x} = 4.20$; $t = 7.04$; $p < .01$).

Phase VI, barriers at 135°. With the barriers at this angle, the model rat, it will be remembered, showed a reversal of discrimination. Somewhat more sound was reflected back to the choice point from the side of the open alley than from the side of the blocked one. The real rats tended to exhibit the behavior predicted from the model. Success on the first block of 20 trials averaged only 40 per cent. The difference of this value from 50 per cent approaches significance ($\sigma\bar{x} = 4.18$; $t = 2.39$; $.10 > p > .05$). The percentages of successful trials for individual Ss during this block were 30, 30, 45, 45, and 50, respectively. As this condition continued, performance improved, though irregularly. A test for linear trend demonstrated that this improvement was significant (df 1 and 30; $F = 8.67$; $p < .01$). Apparently Ss were able to learn to use the reverse cues.

Phase VII, barriers at 90°. Return to the standard condition led to an improvement in mean performance over that of Phase VI ($\sigma\bar{x} = 3.70$; $t = 5.53$; $p < .01$). While the mean performance of 69.90 in this phase was significantly greater than 50 per cent ($\sigma\bar{x} = 2.48$; $t = 7.90$; $p < .01$), it was significantly poorer than the performance under the same stimulus conditions in Phase V ($\sigma\bar{x} = 4.15$; $t = 2.83$; $p < .05$). We interpret the poorer performance as evidence of negative transfer from the reversal of cues during Phase VI. Improvement during the course of Phase VII was significant as a test for linear trend demonstrated (df 1 and 40; $F = 9.18$; $p < .01$).

Phases VIII and IX, sound-producing barriers. In order to determine whether sound that was not produced by the animal might serve as an effective cue, we used barriers that did not reflect sound but, instead, produced it. This barrier was the hardware cloth one, mounted at 45°, and carrying on its back face a small Permo-Flux speaker which emitted white noise. Only the barrier in the closed position emitted noise; the open barrier was silent. The rats showed little evidence of discrimination in Phase VIII, when the sound intensity measured at the choice point was only about 2 or 3 db. above the level of background noise in the experimental room. When the intensity was raised to about 35 db. above the room level in Phase IX, performance improved somewhat. It averaged 63.25 per cent correct during this phase, a value significantly greater than 50

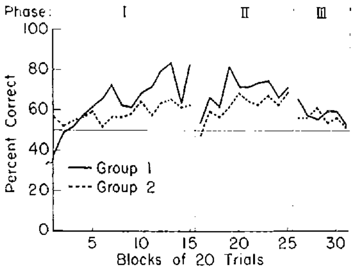

FIG. 4. Per cent correct choices on each block of 20 trials in the supplementary experiment.

	Condition	
Phase	Group 1	Group 2
I	Standard barriers 90° to path	Sound-producing barriers
II	Sound-producing barriers	Standard barriers 90° to path
III	Sound-producing barriers; rats partially deafened	Standard barriers 90° to path; rats partially deafened

per cent ($\sigma_{\bar{x}} = 2.52$; $t = 5.25$; $p < .01$). Apparently *S*s could learn to discriminate under this condition, but there seemed to be little transfer from the previous conditions in which echolocation was possible.

To investigate this point further, we conducted another experiment. These data are summarized in Fig. 4. One group of six rats (Group 1) was first run under the standard condition (solid barrier at 90°) and then with the sound-producing barriers. Another group of six rats (Group 2) was first run with the sound-producing barriers and then under the standard condition. Group 1 had a learning curve similar to that of the animals in the main experiment. (The first part of the original learning data of Group 1 was shown by the dotted line in Fig. 3) Group 2 performed above the 50 per cent level from the start, but their learning was slow, though a test for linear trend demonstrated it to be significant (*df* 1 and 78; $F = 14.59$; $p < .01$). When the cues were switched, so that Group 1 was tested with sound and Group 2 was tested with the standard condition, both groups showed only chance performance on the first block of trials. However, under these changed conditions, both groups improved their performance rather rapidly. Group 1, now with the sound-producing barriers, was again superior to Group 2, as it had been in the first phase of the experiment. The results of this experiment substantiate those of the main experiment, indicating little generalization of cues between the presumptive echolocation condition and the condition in which externally produced sound was the cue. In other words, although the rats could discriminate on the basis of externally produced sounds, they were probably not doing so under the standard condition.

Phase X, barriers at 90°. Return to the standard condition in the main experiment led to an immediate improvement in performance, success averaging 74.40 per cent in this phase. The difference between the mean levels in Phases IX and X was significant ($\sigma_{\bar{x}} = 3.78$; $t = 2.95$; $.02 < p < .05$).

Phase XI, impaired hearing. After the last trial of Phase X, *S*s were anesthetized, and a probe was inserted through each external auditory meatus to break the eardrum and dislodge the ossicles, thus permanently impairing hearing. Performance with the standard barrier in the 120 postoperative trials averaged 55.51 per cent, slightly but significantly superior to 50 per cent ($\sigma_{\bar{x}} = .70$; $t = 7.75$; $p < .01$), but clearly inferior to the performance in the preceding phase. The same operation was performed upon the 12 rats of the supplementary experiment (see Fig. 4), and the performance of both groups declined sharply. With the standard barrier (Group 2), success fell from a mean of 66.25 per cent in the phase before the operation to 56.80 afterward; again, the decrease was significant and to a level only slightly better than chance. Apparently, the impairment of hearing deprived the animals of most of the effective cues in the situation.

DISCUSSION

Returning to our initial question, we have found further evidence in these experiments that the avoidance of the barriers is based on auditory cues. Impairing the animals' hearing entailed an immediate deterioration of performance in each of two groups, and there was no recovery. While success remained slightly above 50 per cent postoperatively, it must be remembered that the animals had not been deafened but had only had their hearing impaired.

Our second question was whether the

effective auditory cues were sounds produced by the rats or were sounds originating from other sources in the environment. (Evidence for either hypothesis is, of course, further substantiation of the dependence of the performance upon auditory cues.) In each of the four experimental conditions pretested with the "model rat," the animals' performance was consistent with the hypothesis that they could detect the barrier only if they could receive from it the echoes of sounds they produced. Sounds originating elsewhere than the choice point can be ruled out as effective cues, for an animal using the echoes of such sounds would have shown a different pattern of successes as the angle of the barriers was changed. Furthermore, since we varied the orientation of the maze in the room daily, we would have varied any extramaze cues. Other than the rat, the only source of sound that kept the same orientation as the maze was *E*, but he stood behind the starting box, and so his sounds would not have been reflected from the barrier back to *S*. Furthermore, neither substituting one *E* for another nor the presence of other people in the room affected the animals' performance. When noise from an external source was employed deliberately to mark the barrier, there was no apparent generalization of cues between this condition and the echolocation condition. We can find no hypothesis other than that of echolocation to account for the results of our tests.

Concerning the nature of the self-produced cues, we have no further evidence than that presented in our preliminary report. Vocal sounds, whether audible to us or ultrasonic, are produced infrequently in the maze, and they do not seem to be related to maze performance. On the other hand, the rats do produce a variety of sounds in the maze—some sniff or even sneeze frequently at the choice point; occasionally they click their teeth loudly; some scratch the floor at the choice point, and the footfalls of most rats can be heard by the nearby observer. It is quite possible that different rats may use different cues, or even that the same rat uses different cues at different times. Work with blind or blindfolded humans has shown that they may use a variety of cues to detect barriers, sometimes without being able to tell what cue they are using. Such cues include footfalls, tapping of a cane on the floor, and snapping the fingers. A small portable click-generator has even been tested as an aid to obstacle location by the blind (2). Since the rat has an abundance of self-produced cues available, it may not be possible to determine which it uses on any specific occasion.

Our results allow us to give a somewhat more complete account than has been given previously of the role of audition in the sensory control of maze performance. Shepard (9) had shown that the flooring of the maze furnished important cues which he believed to be auditory. Tsang (10) confirmed previous results showing sighted rats learned an open maze more readily than an enclosed maze, when both have the same floor plan. He attributed the superiority on the open maze to the opportunity for the use of pattern vision, as had Lashley (6). This interpretation, he suggested, could account also for the fact that enucleation greatly impaired performance in the open maze but had an insignificant effect on performance in the enclosed maze. What Tsang did not consider was the sensory basis for performance when vision cannot be used, i.e., both in the enclosed maze which restricts vision and in blinded animals. We consider it at least suggestive of the possible importance here of echolocation cues that for animals in the enclosed maze, where such cues are undoubtedly available, blinding produced no significant deterioration of performance. In the open maze, which in Tsang's version had no vertical members to provide echolocation cues, blind rats performed far worse than seeing rats and also worse than blind rats in the enclosed maze.

Honzik (4) considered the role of auditory cues by comparing the performance of three groups of rats in an open maze: (*a*) blind rats, (*b*) blind rats for which the maze was rotated 90° or 180° degrees before each run in order to reduce the effectiveness of extramaze cues, and (*c*) blind-deaf rats. The rats of (*b*) performed significantly worse than those of (*a*), indicating that extramaze auditory cues were effective, but they also performed significantly better than those of (*c*), indicating that there were other effective auditory cues. These other cues may well have been echolocation cues, since the structure of Honzik's open maze included vertical panels at the starting box and at the multiple-compartment goal box.

The ability of rats to echolocate suggests that special precautions must be taken in designing experimental situations in which the rat is to be tested. Some experiments already reported might be re-evaluated with this possibility in mind. For example, there is the well-known experiment of Lashley and Russell (7) in which rats raised in the dark were shown, on their first trials in the light, to jump accurately from one platform to another. It is not impossible that the discrimination in this case was auditory, especially since Kahmann and Ostermann (5) have shown a similar ability on the part of dormice and hamsters when visual, olfactory, and position cues were excluded.

In a similar situation we found that several blinded rats would jump 15 to 20 cm. to a platform, but their performance became erratic with greater distances or with long series of trials. As another example of a situation where audition may have played a role, we might cite the experiment of Greenhut (3), who tested for visual distance-discrimination of rats, using movable vertical pegs in enclosed alleys. The *E* considers that the discrimination was visual: "It is highly unlikely that there were any distinctive food odor cues. The *E* always stood directly behind *S* in order to avoid giving any cues inadvertently. With these precautions the discrimination of the 10-in. peg from the 24-in. peg must have been made on a visual basis" (p. 149). But no control was made for auditory cues, so again the possibility cannot be ruled out that the discrimination shown was actually auditory.

SUMMARY AND CONCLUSIONS

Blinded female rats learned to solve this problem on an elevated maze: At the choice point they could go to either of two paths, one or the other of which was blocked by a barrier 20 cm. from the choice point. They learned to avoid the blocked path and detected the barrier from the choice point, evidently by using echoes of sounds they made. Four test situations were designed in which echolocation would yield greater or less success in the maze, and in each case the performance of the animals showed the predicted behavior. Another condition was used in which the rat discriminated on the basis of a noise produced at the barrier, and no generalization of cues could be demonstrated between this and the echolocation situation. When the animals' hearing was impaired, performance was only slightly, though significantly, better than chance would allow.

The ability of rats to echolocate may be the basis of some performances which have been attributed to visual discrimination. This ability should be considered in designing situations in which the rat is to be tested.

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