THE PROPRIOCEPTIVE ABILITY OF THE WHITE RAT[1]

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INTRODUCTION

Since the papers of Watson (8) and Car and Watson (1) it has been widely held that the rat runs the maze purely proprioceptively. Recently this theory has been opposed by much experimental evidence (2, 3, 4, 5, 6, 7). This paper presents further data contradictory to the theory. The present attack upon the problem consists in measuring the capacity of the rat to progress toward a goal with no directive exteroceptive cues beyond the starting box in order to determine whether proprioception by itself is sufficient to enable the rat to run the maze. This differs from the method of my earlier study (3) for in the latter contacts with walls were merely punished, whereas in the present study they were rendered impossible.

EXPERIMENT I

Problem. In the first experiment the rats were required to find a small wire ladder on a large elevated surface in order to reach a pathway leading to food. In order to insure that the problem presented no unusual difficulties to normal animals, the rats were first caused to learn it in the normal condition. They were then blinded. The conditions of the experiment were so arranged that for blind rats there were no directive exteroceptive cues beyond the starting alley.

Animals. Twenty untrained white rats, about ninety days of age at the beginning of training, were used in this experiment. The rats were of Wistar stock.

[1] This paper contains work done under the direction of Dr. Walter S. Hunter of Clark University.

Apparatus. The large elevated surface mentioned previously consisted of a 6 by 14 foot piece of heavy battleship linoleum placed on a smooth board platform of the same dimensions. The linoleum was 12 inches above the floor of the room. Since preliminary experiments showed that rats did not jump down from this height, the linoleum was not enclosed by walls. The platform was mounted on casters in order to make it easy to rotate. Figure 1 shows a ground plan of the apparatus. In this figure the line *X*

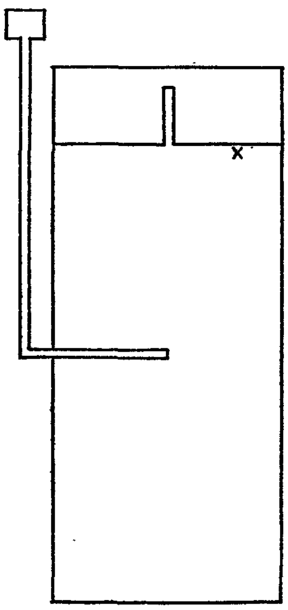

FIG. 1. PLAN OF APPARATUS USED IN EXPERIMENT I

indicates the location of a plank in the middle of which was placed the starting alley as indicated. The starting alley was 3 inches wide, 18 inches long, and 18 inches high. The plank was located 2 feet from the end of the linoleum, and therefore limited the area of the linoleum to which the rats had access to 12 by 6 feet. The wire ladder was situated in the exact center of this area, so that it was 6 feet distant from and directly in front of, the exit of the starting alley. The wire ladder was 4 inches wide and 14 inches long. It was made of heavy $\frac{1}{4}$ inch mesh copper wire and was suspended from the elevated pathway so as to clear the linoleum floor by about ¼ inch. The rats had no difficulty in climbing this ladder. Thd elevated pathway (2 inches wide) was made up of two arms, 4 and 8 feet long, of which the shorter projected over the apparatus. A food platform was nailed to the elevated pathway at the point indicated in the figure.

Procedure. For seven days prior to the beginning of the individual experimentation food was removed from the cages and the rats were placed on the food platform in groups of 5 and permitted to eat and explore the entire apparatus for a half hour. This procedure was followed because the experiment was not designed to secure learning records.

Beginning with the eighth day the rats were placed in the starting box individually and were given 5 trials daily. The rats were fed the McCollum diet, supplemented by occasional greenstuff in their cages. Each rat was allowed to eat a few bites after each run, and was then placed in the starting box for its next trial. When a rat finished its 5 trials, it was placed in a cage until all other rats had finished the day's work, when all rats were fed together on the food platform. (After the preliminary seven days' training the rats did not leave the food platform but fed continuously.) The amount of feeding was adjusted so as to maintain high motivation throughout the experiment.

Time was measured by a stop watch to the nearest second from the moment the rat left the starting alley until it reached the food platform. In order to enable the experimenter to take records of the pathways followed by the rats, a system of radial and circular coördinates was drawn in pencil upon the linoleum, with the middle of the entrance box opening in a center. The radial coördinates were drawn at intervals of 5°, the circular ones at intervals of 9 inches. The rats, when with normal vision, were simply recorded as following or not following a straight line between the opening and the ladder. These performances were called correct and incorrect respectively. The runs of the rats when blind were also recorded as correct and incorrect, but in addition the incorrect runs were further measured as to degree of error by means of the coördinates. The method of measuring the degree of error cannot be outlined until the behavior of the blind rats has been described (under "Results").

The rats were given 20 trials with the apparatus in a fixed position. Beginning with trial 21 the whole apparatus was rotated 45° to the left before each day's trials. Since no extra-apparatus cues retained a fixed position in relation to the true pathway, it was impossible for the rats to direct themselves by means of extra-apparatus cues. After 30 trials of further practice during which the rats had become accustomed to the rotation alternate trials in the light and with the room made dark were given for 10 runs to determine the extent to which the habit was visually controlled. The pathway of the rat, when the room was dark, was observed by attaching a small strip of cloth painted with luminous paint to a piece of adhesive tape and placing this in turn across the back of the rat. This tape remained on the rat during the alternate runs in light. A patch of luminous paint, out of sight of the rats, was placed beyond each corner of the apparatus.

After these tests the rats were blinded and were given 200 trials at the usual rate of 5 per day. Rotation of the apparatus was continued throughout the training of the blind rats. I have noted above that this obviated directive extra-apparatus cues. Since the animals were blind, the only possible exteroceptive directive cues were the tactual, olfactory and auditory stimuli from the apparatus itself. Efforts were made to keep the linoleum surface entirely uniform by daily washing with soap and water, and to all appearances it was at all times uniform. The records to be presented will show that exteroceptive cues, if they existed, were entirely inadequate to normal performance. As a test for exteroceptive cues after the 200th trial of the blind rats 10 trials were given in which the elevated pathway and the ladder were removed and the starting alley was shifted to the opposite end of the linoleum, so that the rats had now to follow a different pathway and reach a different point than had been customary. In these control tests the rats were picked up as soon as they "stopped" as described later.

Results

a. Normal rats. The problem of running directly from the entrance to the ladder presented little difficulty to the normal rats. Learning was nearly completed during the seven days of preliminary feeding. The results secured after this preliminary feeding was presented in table 1. These are presented in chronological order except that the alternate trials in darkness and light are grouped. Confusion when the rotation was instituted indicates that the rats were influenced by the changes in extra-apparatus cues. The return to a high percentage of straight runs indicates, however, that the normal rats could accurately find the

TABLE 1

Performance of 20 normal rats

EXPERIMENTAL CONDITIONS	TRIALS PER RAT	PERCENTAGE OF CORRECT TRIALS	AVERAGE SECONDS PER TRIAL
Apparatus in fixed position	20	90	9.6
Apparatus rotated	5	0	121.3
	15	73	15.6
	10	92	9.4
Darkness	5	0	150.7
Light	5	89	9.8

ladder when no extra-apparatus stimuli were in a fixed position, and, consequently, when extra-apparatus stimuli could not have been directive.

In the dark the rats were unable to find the ladder except by running at random. Once they had found it, however, they climbed up immediately. This behavior was in contrast with that of the first trials after the beginning of rotation, for in the latter the rats often went to the ladder but left it for further exploration of the linoleum.

b. Blind rats. The rats when blinded behaved at first just as they had in darkness, but they gradually learned to find the ladder with much more speed and accuracy than was exhibited on the initial trials. The records of the blind rats which are comparable in nature to those of the normal rats, that is, the records of straight runs and of times, are presented in table 2. This table shows that no improvement was made after the first 50 trials, and that the rats at no time made more than 7 per cent of straight runs in comparison with the record of approximately 90 per cent straight runs which they had made before blinding. The control test showed that the performance of the rats was not controlled by exteroceptive cues from the apparatus. The performance of the rats must therefore have been controlled by the orientation set up in the starting alley.

The rats did not show individual differences great enough to justify the presentation of individual percentages. No rat made as high as 13 per cent straight runs and none as low as 2 per cent

TABLE 2

Performance of 20 blind rats

EXPERIMENTAL CONDITIONS	TRIALS PER RAT	PERCENTAGE OF CORRECT TRIALS	AVERAGE SECONDS PER TRIAL
Normal	50	3	34.3
	50	7	13.4
	50	7	13.8
	50	7	13.2
Control test	10	7	*

* Not comparable.

in any set of 50 trials beyond the first. There was no overlapping between the final performances of the blind and the normal groups.

In order to describe the system of measuring the accuracy of the rats when blind, other than that of recording the runs as correct or incorrect. I must now describe their behavior in more detail. When a blind rat had ceased to improve, its typical performance consisted in a rather straight run from the entrance alley to a point in the direction of the ladder, but seldom to the exact location (only 7 per cent of the time as noted above). This straight section of the pathway was ended by the rat's stopping or hesitating. Beyond this stopping point the rat progressed irregularly, often moving its head from side to side and circling until the ladder was found. The experimenter recorded the rats stopping point to the nearest 5° in direction and to the nearest 9 inches in regard to distance from the entrance by use of the radial and circular coördinates described earlier. This point, together with the constant starting point, defined the straight section of the pathway of the rat.

The relative frequencies of different directions taken by the blind rats in the straight portions of their runs are shown in figure 2. The frequencies approximate those of a normal distribution. It will be seen that the rats went more frequently in the correct direction than in any other one direction (15.1 per cent of

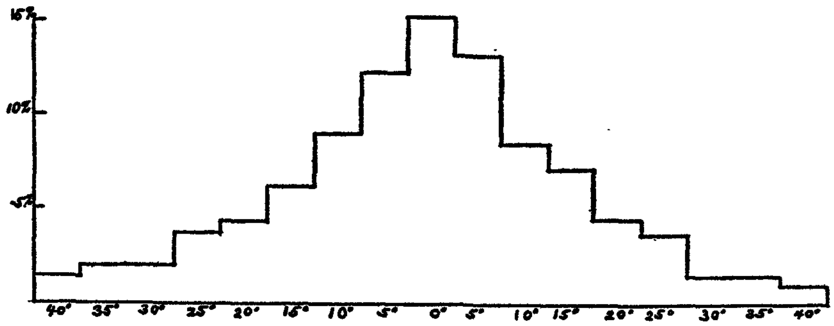

FIG. 2. PERCENTAGE OF THE STRAIGHT PORTIONS OF TRIALS 50–200 OF EXPERIMENT I AT VARIOUS DIRECTIONS TO THE LEFT AND RIGHT OF THE LADDER

the time). (This per cent should not be taken as inconsistent with the somewhat lower per cent of *correct runs* shown in table 2. On some of the runs in which a rat was correct in direction it stopped short of the ladder in distance, and hence made an "incorrect" run.) However, the previous statement that the rats went more often in the correct direction than in any other overstates, in a sense, the accuracry of the rats; for all the errors are divided into two halves, right and left. Figure 3 presents the direction taken as a deviation from the correct direction regardless of whether it was to the right or to the left of the true pathway. This figure shows that deviations of 5° and of 10° from the correct pathway were both taken more frequently by the rats than was the correct pathway itself. The average deviation was 14.8°. In all, these records show an accuracy of performance not at all comparable to the nearly perfect performance of the rats when normal.

The method of recording gave not only the direction of the straight portion of the run, but its distance as well. The length of a correct run was 6 feet. The distance run by the rat before stopping may be compared with this. It should be noted that we

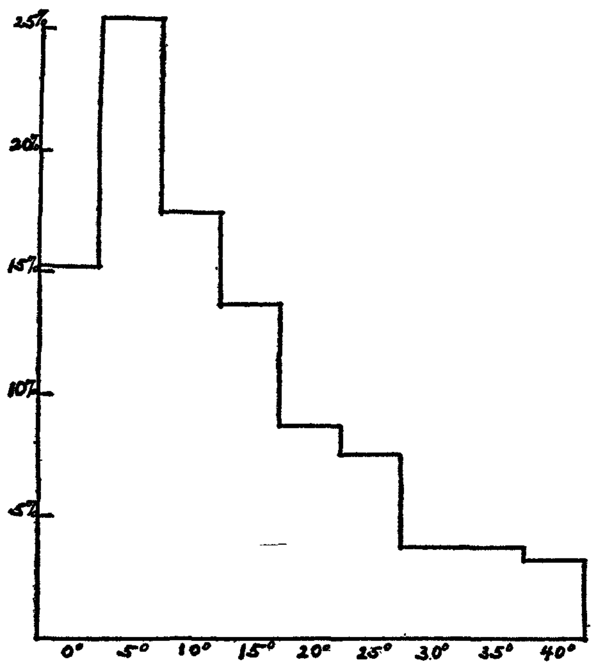

Fig. 3. Percentage of Straight Portions of Trials 50–200 of Experiment I at Various Deviations from the Ladder, Left and Right Deviations of the Same Amount Being Totaled

are not dealing with the distance from the actual position of the ladder at which the rat stopped, but with the distance the rat would have been from the ladder had it gone in the correct direction. Figure 4 presents the results. It will be seen that the rats stopped short of 6 feet in distance more often than they exceeded it, and that only 16.5 per cent of the runs were of the correct length although the readings were taken only to the nearest 9 inches. The average error was 12.08 inches, or about one-sixth of the true distance.

These records of direction and distance do not measure one aspect of the performance of the rats; namely, the behavior beyond the stopping point. After the straight run had ended, the rats still remained for the most part in the general vicinity of the ladder. This behavior was not measured because I was was interested chiefly in straight running, such as is characteristic of maze running.

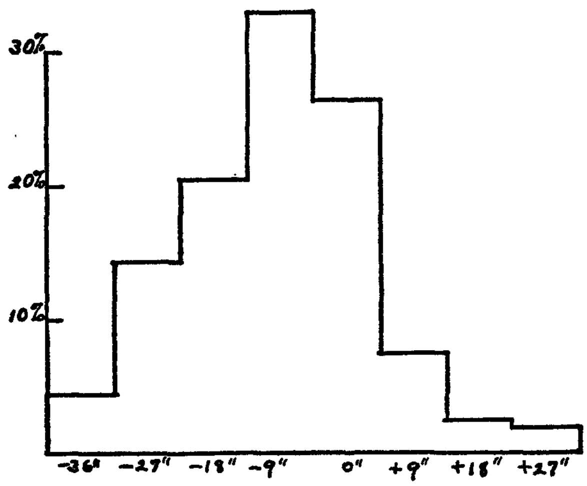

FIG. 4. PERCENTAGE OF STRAIGHT PORTIONS OF TRIALS 50–200 OF EXPERIMENT I AT VARIOUS DEVIATIONS FROM THE CORRECT DISTANCE

EXPERIMENT II

Problem. The second apparatus was designed in order to measure the proprioceptive accuracy of the rat in direction only. The factor of distance was eliminated by building the apparatus in circular form with the starting alley at the center and the goal at a point on the edge, so that all straight paths to the edge of the circle were of the same length.

Animals. The 20 blind rats used in experiment I were used in this experiment after the termination of experiment I. In addition 7 normal untrained rats, ninety days of age, were used for comparison with the blind rats.

Apparatus. The plan of the apparatus is shown in figure 5. A circle of laminated panel 3 feet in radius served as a base for a circle of plain linoleum upon which the rats ran. This circle was placed upon a table 3 feet high. The circle extended beyond the edges of the table at all points, and was not enclosed by walls.

The starting box was 3 inches wide, 12 inches long and 18 inches high. The linoleum circle served as the floor of the starting box. The middle of the opening of the box always coincided with the marked center of the circle, and the starting box always pointed directly toward the food stool. The pointing was made accurate

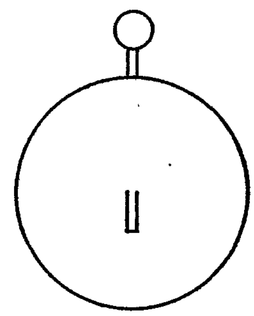

FIG. 5. PLAN OF APPARATUS USED IN EXPERIMENT II

by means of pencil lines on the linoleum. Radii were drawn on the circle at intervals of 5° for recording purposes. Five degrees were represented by an arc of 3.14 inches at the edge of the circle. These lines were drawn in heavy lead pencil.

The food stool was placed 6 inches away from the edge of the circle and was connected to it by means of a 2- by 6-inch plank. This plank was placed against the edge of the circle but was not fastened to it, and did not rest upon the surface of the circle. The food stool was on a level with the circle.

Procedure. The preliminary feeding with exploration of the apparatus was given as in experiment I. Following this, 5 trials per day were given as in the previous experiment. The true pathway was rotated 45° each day. Since the apparatus was circular, it was necessary to change the position only of the starting alley and the food stool in order to accomplish this.

Results

a. Normal rats. The normal rats after from 20 to 25 individual trials ran approximately in a straight path from the starting alley to the food stool. Since they were used only to insure that normal rats would have no difficulty in this performance, their training was discontinued.

b. Blind rats. After the learning period the blind rats followed a fairly straight course from the starting alley to the edge of the circle, but this straight course did not often lead precisely to the

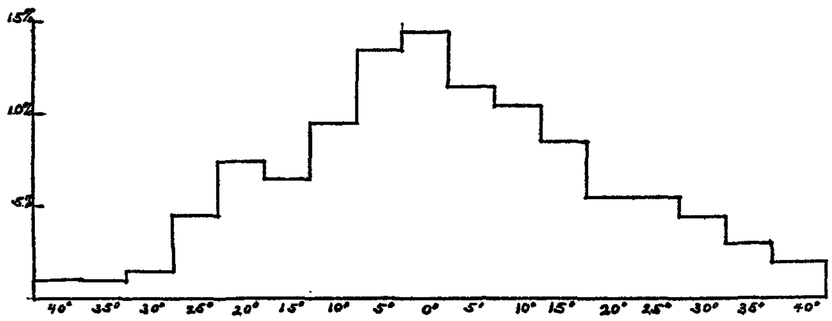

FIG. 6. PERCENTAGE OF TRIALS 35–185 OF EXPERIMENT II AT VARIOUS DIRECTIONS TO THE RIGHT AND TO THE LEFT OF THE FOOD PLANK

food plank. After reaching the edge of the circle at some point other than the food plank, each rat followed the edge of the circle until food plank was found. If in following the edge of the circle the rat turned in the direction away from the plank, it did not continue its direction until it had circled the apparatus but usually turned and retraced its steps after it had gone a short distance.

The angular deviation of the rats from the food plank at the time they reached the edge of the circle was recorded to the nearest 5°. This deviation did not decrease after the first 35 trials, although an additional 150 trials were given. The relative frequencies of the various points first reached on the edge of the circle during the last 150 trials are shown in figure 6. It will be seen that this figure approximates a normal distribution, as did the comparable figure 2 in experiment I. It was not felt necessary to present a figure comparable to figure 3 of experiment I, in that it is clear from the figure here presented that if right and left errors of the same degree were totaled, errors of 5° and 10° would be more common than zero errors. The average error found from figure 6 is 15.2°. This is not reliably different from that found in experiment I, which was 14.8°.

Observation in the present experiment gave no evidence that olfaction in any way guided the rats to the food plank. Often the rats missed the plank by only a few inches. If the plank had offered olfactory cues, there would have been no reason for the rat's failure to locate it accurately from a nearby position. A control test, consisting of removing the food stool and food plank from the apparatus, (the rats were returned to the entrance as they reached the edge of the circle) did not influence the accuracy of the rats.

INTERPRETATIVE COMMENT

Watson, in his well-known monograph (1), p. 93, asks whether blindfolded human subjects could, as rats do, "ever learn to run down the center of the galleries for exactly the proper distances, making the correct turns without in any way touching the sides of the galleries or feeling for the opening?" Probably they could not. But it is obvious from the present study that *rats* are not capable of this performance.

As Hunter has recently written (5), Watson overstated his case. Watson showed that rats could learn the maze when deprived of any one of several non-proprioceptive sensory avenues. In some cases more than one non-proprioceptive avenue were absent at the same time, but in no cases were all non-proprioceptive differential cues absent. As Hunter says (5), p. 460, "There is, however, no evidence that each abnormal rat did not learn in terms of his remaining (non-proprioceptive) sensory avenues."

In the present study an effort was made to do what Watson neglected: to eliminate *all* differential exteroceptive stimuli beyond the starting alley. This has shown the falsity of Watson's conclusions. There is no reason to believe that my apparatus offered a more difficult proprioceptive task than the first alley of a maze. The problem had proved quite easy for normal rats. The blind rats were given many more trials than have ever been required for the learning of any bi-dimensional maze under the same sort of training conditions. Yet the rats were incapable of making more than 7 per cent perfect runs. I conclude, therefore, that the rat cannot run a single alley on a purely proprioceptive basis, except occasionally.

This conclusion should not be surprising. The sensitivity of any receptor must have definite limitations. Rather it is astonishing that a view which demands such perfection of receptor sensitivity as does the proprioceptive theory of maze control should have obtained wide credence.

On the other hand the present paper should not be interpreted to mean that proprioception plays no rôle in maze running. The only contention is that it cannot play a solitary rôle. It is still possible, even, that proprioception may determine entirely the *direction* of turns in the maze; I have shown that it cannot entirely control the *place* of turning and stopping. Vincent (7) reached much of the same conclusion.

The present study corroborates Dashiell's evidence (2) that the rat may maintain an orientation intra-organically. It goes further, and measures the accuracy of performances maintained solely by an intra-organic orientation.

Finally, I wish to add a word concerning the concepts used in this paper. I have used the term "proprioceptive" because the literature on sensory control has used that term (as well as "kinesthetic") to refer to situations such as the present ones. However, in the proprioceptive theory of maze running, the supposedly perfect orientation set up in the starting box is not necessarily proprioceptive in origin. In the present experiments, the blind rat appeared to take its initial direction largely by means of its vibrissae contacts. A large proportion of the final error indirection was present in the initial movement of the rat from the starting alley. This inaccuracy cannot, strictly speaking, be called a proprioceptive error; yet I have so used the term here because the proprioceptive theory of sensory control assumes that the rat can orient perfectly as well as that it can continue without exteroceptive cues. My results refer not to the inaccuracy of proprioception in itself but to the inaccuracy of the proprioceptive theory. They refer not to a situation in which a perfect orientation is given and all error is subsequent, as in experiments with "walking blindfolded," but to a real maze situation which I have described as offering" no differential exteroceptive cues beyond the starting alley."

CONCLUSIONS

With no exteroceptive differential stimuli beyond the starting alley, the rat cannot except infrequently run to a spot a fixed distance ahead as is required by any maze alley. It is certain that the rat cannot run a maze consistently when limited to proprioceptive differential cues. Proprioception may be an important factor in the sensory control of the maze habit, but in any case other cues as well as proprioceptive cues must be present.

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