CORRECTING BEHAVIOR BY INSECTS
ON VERTICAL AND HORIZONTAL MAZES

by

ROGER DAVID AKRE

B. S., University of Minnesota, Duluth, 1960

———————————

A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Entomology

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1962

TABLE OF CONTENTS

INTRODUCTION

This study is concerned with a phenomenon of behavior common to animals that are run in a maze with a 90° forced turn at the end of the starting runway. A short distance beyond the forced turn there is a choice point where one runway continues straight ahead and the other runway (called the "correcting runway") is parallel to and away from the starting runway (Fig. 1). Animals belonging to different phyla have a marked tendency to turn at the choice point and follow the pathway parallel with the starting runway. Animals which turn are said to have "corrected" or exhibited "correcting" behavior (Dingle, 1961). This terminology will be used throughout this paper.

During this study experiments by previous authors were repeated with modifications in attempting to determine causal factors for this behavior. The experimental animals were the red milkweed beetle, _Tetraopes tetraophthalmus_ (Forster), and the yellow mealworm, _Tenebrio molitor_ Linnaeus.

LITERATURE REVIEW

The literature on "correcting" behavior includes primarily papers on rats with a few studies on insects and other animals. Although correcting is shown by a wide range of animals, Rice and Lawless (1957) reported that a flatworm did not show this behavior. The three major hypotheses suggested to explain this type of behavior are here designated (1) successive induction, (2) centrifugal swing, and (3) reactive inhibition.

The first, "successive induction", proposed by Sherrington (1906: 214) states that after an animal has made a forced turn in a maze there would follow "a compensatory reflex, which brings the moving parts back again to

the original position of equilibrium." Therefore, if an animal is forced to turn or inhibited from continuing in a fixed direction this inhibition would be "followed by a rebound to superactivity" which would take the animal on a course parallel to the starting runway at the choice point.

Dashiell and Bayroff (1931) suggested another theory to explain the tendency of animals to correct. They called it "forward-going tendency" and described it as follows:

> It seems likely that the factor most responsible is a forward-going tendency in animal locomotion that leads not only to maintenance for short distances of a direction already set but also to a compensatory sort of correction when forced out of line by an obstruction.

This author considers this merely a restatement of the theory of successive induction suggested by Sherrington.

The second hypothesis advanced to explain correcting behavior is that of centrifugal swing suggested by Schneirla (1929:69) in a paper on ants. Schneirla states,

> In general, it depends upon the physical fact that in passing around a corner with reasonable speed, the animal must run near the outside walls of the turns, until compensatory movements restore the normal center of equilibrium. While the ant is under the influence of this centrifugal swing, movements compatible with it (turning into /an alley on the same side as the outside of the turn/, for example) will be easily made.

Witkin and Schneirla (1937) defended the concept of centrifugal swing against that of forward-going tendency and stated that the latter is "incomplete and in many ways actually inconsistent with the facts of choice point behavior." Correcting behavior was also shown by German cockroaches (Hullo, 1948) and by white rats (Ballachey and Buel, 1934) and was interpreted on the basis of centrifugal swing.

The third hypothesis is the principle of reactive inhibition (Hull, 1943:278). According to this concept the occurrence of a response reduces temporarily the probability of its recurrence. Therefore, the probability of an animal turning in the opposite direction from the forced turn is great.

Lepley and Rice (1952:283) extended and reformulated this Hullian postulate as follows:

> When any reaction occurs, the probability of its later occurrence is reduced. The probability of its later occurrence increases with the continuing succession of following, dissimilar reactions. It is proposed that the probability of later occurrence would be reduced progressively with continued repetition; and that the degree of reduction would be proportioned to the degree of repetitiousness. It is further proposed that this reduction in the probability of occurrence for a particular reaction would enhance the probability of occurrence for other actions in the Repertoire.

In an experiment reported as supporting reactive inhibition in yellow mealworms (Grosslight and Ticknor, 1953), the "opposite turning tendency" (correcting) was found to be decreased as the length of the pathway from the forced turn to the choice point was increased. The closer the choice point is to the forced turn the greater the probability of an animal making an opposite turn, making the spatial arrangement of the alleyways very important in this theory as in the centrifugal swing theory. Studies on Paramecium (Lepley and Rice, 1952), and on rats (Zeaman and House, 1951) produced results that were interpreted as supporting reactive inhibition. Glanzer (1953) studied the maze running of rats and found a similar pattern of behavior in which the rats tended to alternate their paths at the choice point from trial to trial. He suggested this behavior, called "spontaneous alternation", could be explained by response-oriented theories such as reactive inhibition.

In a modified retest of the Grosslight and Ticknor study, Grosslight
and Harrison (1961) controlled some factors previously overlooked. V-shaped
alleyways were used to control thigmotactic influences by having both
sides of the body of the animal constantly touching the sides of the
alleyway. The V-shaped alleyways also minimized the possibility of
centrifugal swing. Because of the controls used, the authors concluded
that their results were consistent with the reactive inhibition hypothesis
and that the alternative hypotheses of centrifugal swing and thigmotaxis
were untenable.

Dingle (1961) found that time, measured by running speed between the
forced turn and the choice point, was independent of the correcting by
boxelder bugs. However, as the distance between the forced turn and the
choice point was lengthened, the amount of correcting decreased.

MATERIALS AND METHODS

Red Milkweed Beetle, Tetraopes tetraophthalmus (Forster)

Experimental Animals. Approximately 5,000 red milkweed beetles were
collected between June 15 and August 3, 1961, in a small field of milkweed
2 miles north of Manhattan, Kansas, on Highway 13. Initially 500 beetles
could be collected in 30 to 45 minutes, but between August 3 and 15 the
beetles rapidly decreased in number and then disappeared almost entirely,
terminating further collections and experiments.

Because the beetles will bite off parts of appendages if 2 or more
beetles are placed in one container, each specimen was put in a 5 ml. plastic
vial. At the laboratory one-gallon jars containing 2 to 4 crumpled paper
towels were used to hold about 50 beetles each. The towels gave the beetles

firm footing and reduced the amount of injury due to biting. In spite of
the precautions taken, most of the beetles lost parts of their legs within
10 days. Fresh milkweed leaves were added to each jar every other day.
Between experiments the gallon jars containing the beetles were placed on
a shelf in the laboratory and stored without controlling the light conditions.

Mazes. All the mazes used with the red milkweed beetles were
constructed of balsa wood except for one made of plastic. Balsa wood was
used for ease in fabricating mazes and because it gave the beetles firm
footing. The wood strips except one (Fig. 10) were 6 mm. square and were
held together by glue and pins. This width runway was selected because as
the beetles walked their legs just rested on both edges. The patterns and
dimensions of all the mazes are given in Figs. 1 to 10. Each maze was
suspended within a rectangular balsa wood frame (Fig. 6,b) by fine black
silk thread tied to screw eyes. Each frame measured 45 cm. x 32 cm. except
one (Fig. 6) which was 50 cm. x 32 cm. Each maze could be used in a vertical
or horizontal position. When used horizontally a support (Fig. 8) was used
to raise the runway up to the level of the light. This support brought the
runway directly up to the middle of the light container. Suspending the
runway in the air was necessary to prevent the beetles from crawling off the
runway. The last horizontal maze (Fig. 9) was built of Plexiglas in the
form of rectangular tunnels through which the beetles would just fit with
their bodies touching both sides of the runway. After the maze was con-
structed at least 24 hrs. were required to eliminate the odor of the cement
solvent.

Light Source. The beetles were attracted toward a light placed along
the narrow edge of the frame opposite the starting point of each maze. The

source of light was an adjustable fluorescent desk lamp containing 2, 15-watt bulbs 41.5 cm. in length. The 2 parallel bulbs were 1.5 cm. apart, and the edge of the frame was centered between the 2 bulbs when the maze was used in either a vertical or horizontal position. The whole bulb container could be switched end for end to eliminate possible light bias. Experiments performed in "darkness" were done using dark red light just strong enough to make it possible to see the beetles. Although the red milkweed beetles were strongly attracted to daylight and fluorescent lights, a test showed the beetles were not attracted to the red light used.

Other light was minimized by enclosing the light and maze on all sides by black cardboard screens except on the side toward the observer. When the maze was vertical, the observer faced one flat side of the maze; and when the maze was horizontal, the observer faced one end of the horizontal maze support (Fig. 8). The screen enclosure for vertical runways measured 48 cm. wide, 48 cm. high, and 38 cm. deep. That for horizontal runways measured 48 cm. wide, 30.5 cm. high, and 56 cm. deep.

Procedure. The beetles were examined before they were placed on each maze, and those missing parts of legs and antennae were rejected. Even if only the tarsal claws were missing, the beetles were rejected because they had difficulty holding onto vertical runways.

After a beetle was placed on the maze it could be rejected if it (1) paused more than 5 seconds at any choice point or along any runway, (2) flew after walking part of the runway, or (3) went down the string at the forced turn. None of the rejected beetles was put back at the starting point. Except where other data are given below, the beetles were counted whether they ran on the front, back, or sides of the runway. After traveling

one body length along a runway at a choice point, the beetles were counted
as having traveled that runway. At several equal intervals during certain
experiments the mazes were turned 180 degrees to eliminate possible bias
which might result if the forced turn was always toward the same side.
At different intervals the light was also turned end for end.

Yellow Mealworm, Tenebrio molitor Linnaeus

Experimental Animals. All of the mealworms were kept in jars of
wheat flour in a dark closet when not being used in the maze experiments.
At least 30 minutes before running the mealworms on a maze, the mealworms
were sifted out of the flour in which they were kept and placed under a
fluorescent desk lamp with 2, 15-watt lights to make them active. At this
time any mealworms that were molting, had just molted, or were otherwise
sluggish were picked out and discarded for testing purposes. Only mealworms
were used which were large enough that both sides of their bodies touched
the sides of the runways.

Mazes. All of the mazes were made by cutting runways 3.5 mm. wide and
5.0 mm. deep into plaster of Paris blocks 3 cm. thick. A screwdriver, ground
to a width of 3.5 mm., was used to cut the runways. After the runways were
cut, a light coating of beeswax was painted over the entire surface of the
block to make it more durable and to make the surfaces of the runways smooth
and nonpowdering. Then the screwdriver was heated and drawn through the
runways to smooth out any irregularities. The patterns and dimensions of
these mazes are illustrated in Figs. 11 to 14. Where some of the runways
continued to the outside edges of the plaster block (Figs. 12 & 13), small
cardboard boxes were placed against the open ends. It was thought that these

boxes minimized error which could result if runways with open ends appeared
lighter than those with closed ends or turns.

Light Source. The mazes were placed on a horizontal surface with a
150-watt reflector flood lamp suspended over the middle of the maze. The
distance from the top surface of the maze to the bottom of light was 75 cm.

Procedure. Mealworms placed in the runway were discarded if they
(1) hesitated more than 5 seconds at any point in the maze, (2) turned
on their sides between the forced turn and the choice point, or (3) crawled
out of the runways. The mealworms were counted as having traveled a runway
after they had proceeded one body length down that runway.

RESULTS

Red Milkweed Beetles

Vertical Mazes. Red milkweed beetles were first tested on Maze 1 to
determine the proportion of correcting. All of the beetles that were used
were "naive" beetles or individuals that had never run any maze previously.
The results for 500 beetles are given in Table 1. The hypothesis that the
beetles followed the runways at the choice point in a 1:1 ratio was tested
by chi-square, and this test indicated a highly significant amount of
correcting ($P < 0.001$).

Maze 1 was used again to see if sight was important for the proportion
of beetles correcting. As stated above, light in front of the maze attracts
the beetles so that they run quickly over the maze. The beetles were tested
on Maze 1 under dark conditions except for a dim red light shining on the
lower right corner of the maze. The beetles were not attracted to this light
and probably could not see it. Under these "dark" conditions there were

many more rejections (23) compared with previous tests. Since only 47.5% of 200 beetles which ran the maze corrected, the probability is greater than 0.40 that the choice of runways fit a 1:1 ratio (Table 1).

Beetles with their compound eyes covered with black paint were run over Maze 1, and the results were similar to those from the experiment done in the dark. Only 44.5% of 200 beetles corrected (Table 1).

Next the beetles were run over Maze 1 with their left antenna cut off. The maze was positioned so that the runway parallel with the starting runway turned left. Therefore the left antennae would have normally touched this runway as the beetles walked over the maze. Under these conditions 67 of 100 beetles corrected. Another 100 beetles were run with both antennae cut off. Only 49 out of 100 corrected. Comparing the ratio of correcting in the first experiment with Maze 1 (392 corrected, 108 did not) with the proportion of correcting in Maze 1 with one antenna cut off and with both antennae cut off gives the chi-square values of 6.02 (P <0.02, comparing the ratios 392/108 to 67/33) and 36.98 (P <0.001, comparing the ratios 392/108 to 49/51) indicating that the 2 ratios obtained with antennae cut off are significantly different from the first ratio. These data show that the incidence of correcting is lowered when one or both antennae are amputated (Table 1).

Mazes 2, 3, and 4 were constructed to see what effect lengthening the runway from the forced turn to the choice point would have on the correcting of the beetles. The distances between the forced turns and choice points were 5, 7, and 9 cm. respectively. The results given in Table 1 indicate that the probability of correcting decreases rapidly with the distance from forced turn to choice point.

Table 1. Amount of correcting by red milkweed beetles.

	Total Number	Number Correct- ing	Percent Correct- ing	Chi- square	P
Vertical Mazes					
Maze 1	500	392	78	160	< 0.001
dark	200	95	47.5	.5	> 0.40
eyes painted black	200	89	44.5	2.45	> 0.10
1 antenna cut off	100	67	67	5.78	< 0.02
2 antennae cut off	100	49	49	.04	> 0.80
Maze 2	500	312	62	31.5	< 0.001
Maze 3	500	271	54	3.52	< 0.10
Maze 4	500	258	52	.51	> 0.30
Maze 6					
A	480	433	90	310	< 0.001
B	433	403	93	323.8	< 0.001
Maze 7					
beetles previously collected					
A	100	75	75	24.8	< 0.001
B	100	74	74	23.04	< 0.001
beetles freshly collected					
A	100	78	78	31.36	< 0.001
B	100	22	22	31.36	< 0.001
Horizontal Mazes					
Maze 1	100	78	78	31.36	< 0.001
maze painted black	100	71	71	17.64	< 0.001
eyes painted black	100	31	31	14.72	< 0.001
dark	100	40	40	4.0	< 0.05
Maze 7					
A	100	73	73	21.16	< 0.001
B	100	24	24	27.04	< 0.001
Maze 8	100	82	82	40.96	< 0.001
Maze 9	100	63	63	6.76	< 0.01
Maze 10	100	56	56	1.24	> 0.20
Maze 11	100	69	69	14.44	< 0.001

EXPLANATION OF PLATE I

Figs. 1-7. Maze designs.

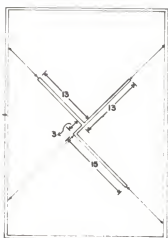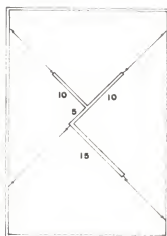Fig.   8. Suspending frame. All dimensions
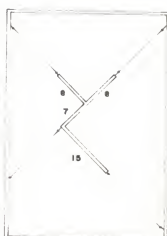   are centimeters.

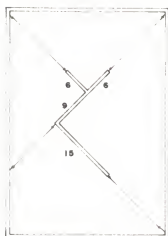PLATE I

Fig. 1 Maze 1
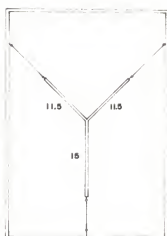
Fig. 2 Maze 2

Fig. 3 Maze 3
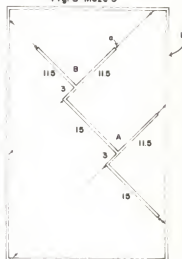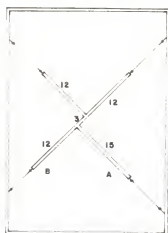
Fig 4 Maze 4

Fig. 5 Maze 5
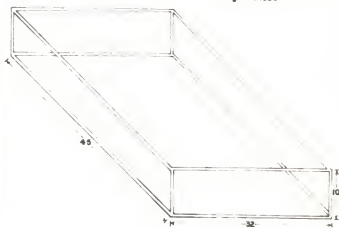
Fig. 6 Maze 6

Fig. 7 Maze 7

Fig. 8

The beetles were run on Maze 5, a simple Y-maze, to see if there was any bias for turning either right or left under the conditions for vertical mazes. The maze was turned 180° so that the left arm of the Y would be where the right arm of the Y had been after each of 4 groups of 50 beetles were run. The ratio of 103:97 gave a chi-square value of $P > 0.50$ which indicated that the choice was not significantly different from a 1:1 ratio. Thus, there should have been no bias due to uneven lighting in the experiments where the beetles corrected.

Maze 5 was also used to provide more information on how the antennae influence the choice of turn. When the beetles came to the choice point of the Y, they were observed closely to see whether the runway touched first by an antenna or tarsus was the one selected. A total of 189 beetles were placed on the maze and of these 93 turned left and 96 turned right at the choice point. Of the 93 beetles turning left at the choice point 37 touched their left antenna to the left runway first and 51 touched the left runway with their left front tarsus first. The remaining beetles either touched the right runway with either tarsus or antenna first, or they were not observed. The beetles which took the right runway at the choice point gave similar results. Twenty-eight of the beetles contacted the right runway first with their right antenna, and 53 touched the right runway first with their right front tarsus. The remaining beetles touched the left runway in some manner before turning right, or else the results could not be observed. All beetles which did not run the front face of the runway were rejected and not counted.

Maze 6 (Fig. 6) was constructed to see if the beetles would correct twice in rapid succession. The values obtained for Maze 6 are shown in

Table 1. These values are based on 480 beetles being started at the bottom
of the maze. Of the 480 beetles run 433 or 90% corrected once, and 403 or
93% of the 433 beetles corrected twice.

The last maze to be used vertically, Maze 7, had 2 starting runways,
A and B (Fig. 7). From starting point A, 75 of 100 beetles corrected, while
74 of 100 beetles from starting point B turned at the same choice point. In
repeating this experiment with freshly collected beetles, the results were
altogether different. Only 22 of 100 beetles started at B took the
"correcting runway". From starting runway A, 78 of 100 corrected, almost
identical to the previous experiment.

Horizontal Mazes. When Maze 7 was used horizontally, the results
were similar to those from the second series of freshly collected beetles
on this maze used vertically (Table 1). During this experiment even
though a beetle walked on the left side of runway B, it more frequently
climbed over the branch runway and continued straight rather than turning
left at the choice point.

Beetles tested on the horizontal Maze 1 corrected to the same degree
as when the maze was vertical (Table 1). Maze 1 was then reused in 3 other
experiments. First the maze and all of its supporting framework was
painted black to see if this would influence the beetles' behavior at the
choice point. Since 71 of 100 beetles run over the maze corrected, the
black runways did not seem to influence the correcting of the beetles.
Next 100 beetles whose eyes had been painted out with black paint were
placed on the same maze. Only 31 of these 100 beetles corrected. Since
the beetles corrected much less often with their eyes covered, it was assumed
that they would react the same in the dark. To test this hypothesis, 100

beetles were run over the maze using only the red light for illumination. Only 40 of 100 beetles corrected (Table 1).

Maze 8 (Fig. 10) was exactly the same dimensions as Maze 1 except that the runways were widened from 6 mm. to 14 mm. Since 82 beetles of 100 corrected, it appeared that the width of the runways influenced the amount of correcting. Additional tests would be required to determine whether this difference is significant.

Shortening the starting runway decreased the amount of correcting to approximately the same degree as increasing the runway between the forced turn and choice point in Mazes 2 to 4. In Maze 9 with a starting runway of 10 cm. only 63 of 100 beetles corrected, and 56 of 100 corrected on Maze 10 with a starting runway of 5 cm. (Table 1).

Maze 11 (Fig. 9), the last maze to be used horizontally, was constructed to provide constant thigmotactic stimuli on both sides of the beetles and to minimize centrifugal swing. The maze was placed on top of a framework similar to that in Fig. 8 except with cross bars placed 1 cm. apart across the top. The ends of the Y of the maze were positioned so that they were exactly 13 cm. from the end of the light. The maze was placed as illustrated in Fig. 10, with the forced turn toward the right. After 50 beetles were run the maze was turned over so the forced turn would be to the left; and a second group of 50 beetles were run. Thirty-five of the first and 34 of the second group corrected. More of the beetles would have corrected if they had not had difficulty turning into the runway parallel to the starting runway. Twelve beetles started to make this turn but backed out and continued along the straight tunnel. In spite of this problem a significant percentage of the beetles corrected.

Yellow Mealworms

Mealworms were first tested in Maze 12 (Fig. 11) which was almost identical to the basic design used by Grosslight and Harrison (1961) except that the starting runway was 6 cm. long. After the choice point the ends of the runways gradually sloped to the surface to allow the mealworms to crawl out of the runway where they could easily be picked up with forceps. The maze block was oriented in the 4 major quadrants and 25 mealworms were run in each quadrant to eliminate any bias due to uneven lighting. A highly significant total of 91 of 100 mealworms corrected (Table 2). Only 5 mealworms were rejected for various causes.

Mealworms were released just beyond the forced turn to determine if their choice of runways at the choice point was 50:50. Twenty-five mealworms were run in each of the 4 quadrants, and the sums of the choices (49:51) showed no significant deviation from 50:50 (Table 3).

Maze 13 (Fig. 12) with a pattern comparable to Maze 1 was also used to test the amount of correcting by mealworms. This maze was also oriented in the 4 major quadrants and 50 mealworms were run in each quadrant. Out of 200 mealworms 154 or 77% corrected. A chi-square test against the hypothesis of a 50:50 choice is significant at the level $P < 0.001$. Actually these data give a conservative estimate of the degree of correcting; because when mealworms were released in the maze just beyond the forced turn, it was clear the choice is not 50:50. Forty-four of the insects went straight ahead out the maze and only 6 turned into the correcting runway.

Maze 14 (Fig. 13) was constructed to determine if the mealworms would correct more than once. First the choice points were tested to make sure that there was no bias present for a right or left turn due to an error in

Table 2. Amount of correcting by yellow mealworms.

	Total Number	Number Correcting	Percent Correcting	Chi-square	P
Maze 12	100	91	91	67.24	< 0.001
Maze 13	200	154	77	58.3	< 0.001

Table 3. Pretests of parts of mazes and test of significance from 50:50.

	Number	Left	Right	Chi-square	P
Maze 12	100	49	51	0.04	> 0.80
Maze 14 A	1000	519	481	1.44	> 0.10
14 B	100	51	49	0.04	> 0.80
14 C	100	50	50	0.00	1.00
14 D	100	53	47	0.36	> 0.50
14 E	100	48	52	0.16	> 0.50
Maze 15	500	276	224	5.40	< 0.025

Table 4. Analysis of segments of Maze 14 based on 1,000 mealworms started at base point A.

Routes for Analysis	Number At Point Given	Corrected	Percent Corrected	Chi-square	P
A-B-D	519 (B)	446 (D)	86	366.12	< 0.001
A-C-E	481 (C)	403 (E)	84	221.40	< 0.001
B-D-G	446 (D)	285 (G)	64	34.43	< 0.001
C-E-J	403 (E)	219 (J)	54	3.22	> 0.05

Table 5. Analysis of segments of Maze 15 based on 500 mealworms started at base point A.

Routes for Analysis	Number At Point Given	Corrected	Percent Corrected	Chi-square	P
A-B-C	276 (B)	184 (C)	67	30.67	< 0.001
A-E-G	224 (E)	165 (G)	74	50.02	< 0.001

EXPLANATION OF PLATE II

Figs. 9-14. Maze designs. All dimensions
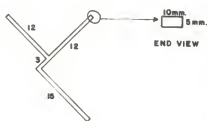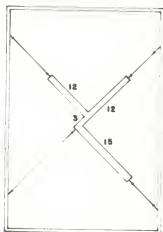   are centimeters.
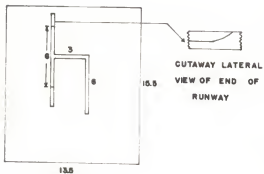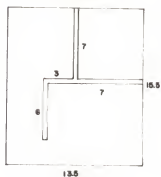
PLATE II

Fig.9
Maze 11

Fig.10 Maze 8

Fig.11 Maze 12

CUTAWAY LATERAL
VIEW OF END OF
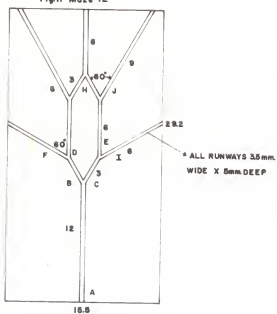RUNWAY

Fig.12 Maze 13
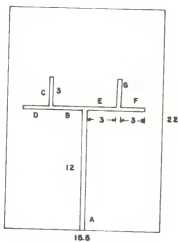
ALL RUNWAYS 3.5mm.
WIDE X 5mm DEEP

Fig.13 Maze 14

Fig.14 Maze 15

the construction of the maze. One hundred mealworms were released at each point; B, C, D, and E (Fig. 13) and their choices at each Y are recorded in Table 3.

Since none of these results indicated that any of the choice points deviated from a chance probability of 50:50, the maze was assumed to be constructed correctly, and mealworms were run over the maze from the starting point at the bottom. The results of 1,000 "naive" mealworms running the maze are given in Table 4. Even though in this maze none of the turns were 90° angles, a significant amount of correcting was shown when each segment of the maze was analyzed separately.

The last maze used with the mealworms, Maze 15 (Fig. 14), was used to provide additional data for correcting behavior. Five hundred mealworms were started at the bottom of the maze, and 276 turned left (B) and 224 turned right (E). The results indicated a highly significant amount of correcting (P < 0.001, Table 5).

DISCUSSION AND CONCLUSIONS

In running milkweed beetles over the vertical mazes an apparent error was present which should be clarified. The milkweed beetles were always placed on the bottom of the starting runway on the side of the runway facing the observer. The beetles would usually run on this face of the runway until they reached the forced turn. At this time they would get on the top edge of the runway and in continuing up the maze would run into the correcting runway. This can be considered a form of "centrifugal swing" in that the beetle's forward momentum carries it over the forced turn so that the beetle runs into the correcting runway. In addition, it is easier

for the beetles to run on an upper surface of a runway instead of on a
vertical surface. This same problem was present when the milkweed beetles
ran on the horizontal mazes. They would over-run the forced turn; and
before they could climb back to the top of the maze runway, they would run
into the correcting runway.

The above behavior would seem to invalidate the results obtained,
at least on the vertical mazes. Yet when the forced turn to choice point
distance is lengthened from 3 cm. to 5 cm. or more on the vertical mazes
the proportion of beetles correcting markedly decreases. Yet the beetles
were still walking on the upper surface of the runway and running directly
into the correcting runway. The majority of the beetles merely walked
around this runway and continued straight ahead when the distance from the
forced turn to choice point was lengthened beyond 3 cm.

In one case when the milkweed beetles "bumped" head on into the
correcting runway, a majority took this runway. This behavior was present
when Maze 7 was used in a vertical position with red milkweed beetles which
had been kept in the laboratory but was not present with recently collected
beetles. For some unknown reason, the insects' behavior was modified by
keeping them in the laboratory for approximately one week. The beetles
moved more slowly than freshly collected beetles and in other ways exhibited
peculiar behavior, such as moving erratically instead of in a straight line,
falling off the runways more often than fresh beetles, and in other ways
appearing uncoordinated. Perhaps this unusual behavior resulted from eating
paper or from oxygen starvation in the bottom of the jars. Because of these
changes in behavior, all the other milkweed beetles used in this study were
freshly collected.

Increasing the length of the starting runway increases the probability of correcting. This result was obtained using horizontal mazes but almost certainly would also be found with vertical mazes. The increase in correcting may be attributed partly to a greater running speed increasing the amount of centrifugal swing. Although all the runs were not timed, it was clear that a high proportion of the beetles run on the mazes with long starting runways corrected. The concepts of centrifugal swing, successive induction, and reactive inhibition offer no interpretation of this effect.

Maze 15 was similar to Maze 13 except that the starting runway was 12 cm. long compared with 6 cm. for Maze 13. This longer starting runway should have increased the amount of correcting but it did not. Comparing the ratios of mealworms which corrected and did not correct in both mazes (154/46 to 349/151) gives a chi-square of 3.57 ($P > 0.05$) indicating that the ratios are not significantly different from each other. Perhaps the length of starting runway exceeded the distance beyond which there would be no more increase in correcting behavior.

Increasing the distance between the forced turn and the choice point decreases the probability of correcting. This result could be attributed to centrifugal swing, successive induction, reactive inhibition, or any combination of these principles.

It is interesting to note that a difference of 2 cm. in either the length of the starting runway or between the forced turn and choice point was all that was needed to change from a significant to a nonsignificant amount of correcting when tested against the hypothesis of a 50:50 choice. This length is just slightly greater than the length of the beetles.

The amount of correcting in Maze 6 not only was very significant but it appeared to be much higher than in Maze 1 although beetles freshly collected were used on both mazes. A chi-square value of 25.4 (P < 0.001) indicated that the proportion correcting at the first choice point was significantly different from the proportion correcting in Maze 1 (the ratio 392/108 as compared to the ratio 433/47). The greater proportion of correcting in Maze 6 may be due to the fact that the maze continues up higher from the first correcting runway (Fig. 6,A) than from the alternate route. If the beetles saw this, it may have influenced their choice of runway. Since the 2 top alternate routes carry the beetles to equal heights, this would not apply to the second choice point and still a greater number of beetles corrected here than on Maze 1. A chi-square value of 39.85 (P < 0.001) indicated the 2 ratios were significantly different from each other (403/30 compared to 392/108).

Increasing the width of the maze runways from 6 mm. to 14 mm. seemed to increase the amount correcting, but too few beetles were available to determine if this difference was significant. With the wider runway the beetles were in contact longer with the correcting runway, and many beetles walked nearly all the way across this runway before stopping, turning, and walking up the correcting runway.

When the milkweed beetles were tested in darkness or with their eyes covered with black paint, less than 50% of the beetles selected the "correcting runway". These results may be attributed to several factors. (1) The beetles could not see the correcting runway so they continued straight ahead, (2) the beetles were more hesitant and walked much more slowly, and (3) largely as a result of walking slowly, the beetles did not over-run the forced turn as frequently, and thus, more often followed the

edge away from the correcting runway with which they had no physical contact.

Maze 1 in a horizontal position was tested to determine if the 2 alternate runways at the choice point had a 50/50 probability. To test this 100 beetles were released beyond the forced turn and 92 of 100 continued straight ahead. This indicates that the choice is not actually 50/50 and that the beetles with their eyes covered still may have exhibited correcting behavior to some extent even though less than 50% corrected.

In an attempt to control centrifugal swing the beetles were tested in Maze 11 made of rectangular tunnels in which the beetles would just fit with their bodies touching both sides of the runways. A significant number of the beetles corrected in this maze. A uniform thigmotactic stimulus on both sides of the beetles should have been present at least up to the choice point. Since the beetles walked through the maze very slowly and with difficulty, there must have been a minimum of centrifugal swing forcing the beetles to the side of the correcting runway. However, the beetles still tended to press against the wall on the side of the correcting runway more than the other wall after the forced turn. It is thought that this type of "centrifugal swing" is impossible to control in any maze design.

In all the experiments involving yellow mealworms the mazes were constructed to minimize centrifugal swing and unequal thigmotactic stimuli. As in the case of red milkweed beetles, centrifugal swing could not be controlled entirely. The mealworms also tend to press their bodies more strongly against the opposing wall than the other wall when forced to turn. This must have affected the proportion of mealworms which corrected.

On Maze 14 the mealworms corrected less the second time than they did the first time. On the right side of the maze (J) the choice by the mealworms was close to a 1:1 ratio ($P > 0.05$). If the bottom arms of the maze (B,C) had been lengthened to 5 cm. or more this might have increased correcting at the last choice point. This would also probably decrease the correcting at the first choice point by increasing the distance from the forced turn to choice point. Reducing runways D and E to 3 cm. should also result in a higher proportion of mealworms correcting the second time. On the other hand, if the number of mealworms correcting on both the right (J) and left (G) sides are added together and treated as one; 504 of 849 mealworms corrected the second time. This gives a chi-square of 29.37 and correcting is significant at the $P < 0.001$ level.

Maze 14 and 15 are similar in construction in that each has a 12 cm. starting runway and 3 cm. forced turn to choice point distance. In comparing the proportion of correcting in these mazes only choice point number 1 was considered in Maze 14. By adding the mealworms which corrected on both sides of Maze 15 the ratio of 349 corrected and 151 did not is obtained. A similar ratio (849 to 151) is obtained by adding the mealworms which corrected and which did not correct at the first choice point of Maze 14. A chi-square value of 47.33 ($P < 0.001$) indicates that these ratios are significantly different from each other. Compared with Maze 15 a much greater proportion of mealworms corrected at the first choice point of Maze 14 probably because the mealworms had to turn only $30°$ angles rather than $90°$ angles.

Mazes 12 and 13 were compared in a similar manner. The ratios of correcting and noncorrecting were compared (91/9 to 154/46) and the chi-

square value was 8.74 (P < 0.01). Maze 12 had a greater proportion of mealworms correcting than Maze 13. The probable explanation for this behavior is that the mealworms had to turn right or left in Maze 12 whereas in Maze 13 they could continue straight ahead.

This demonstration that correcting behavior also occurs on vertical runways suggests that this behavior may be important in nature. Some nonrandom distributions of insects on plants may be based in part on correcting by insects walking up from the bases of the plants.

SUMMARY

This study concerns the behavior of the red milkweed beetle, _Tetraopes tetraophthalmus_ (Forster), and the yellow mealworm, _Tenebrio molitor_ Linnaeus, on simple mazes. Both insects after a forced turn "correct" their direction of running by choosing a runway parallel with the starting runway. Sight, antennae, width of runway, distance from forced turn to choice point, and the length of the starting runway all influenced the proportion of red milkweed beetles which corrected on either horizontal or vertical mazes. Schneirla's concept of centrifugal swing appeared to be most useful for interpreting the results. Experiments with milkweed beetles or mealworms in runways with walls touching the sides of the insects showed that centrifugal swing could not be entirely controlled in any of the maze designs used in this study. The principles of reactive inhibition (Hull, 1943) and successive induction (Sherrington, 1906) are also discussed.

It is suggested that correcting behavior may result in some nonrandom distribution of insects on plants.

ACKNOWLEDGMENTS

I wish to thank my major professor, Dr. Carl W. Rettenmeyer, for his untiring suggestions and assistance.

The author wishes to express sincere appreciation to Dr. Herbert C. Knutson, Professor and Head, Department of Entomology, for his interest in and promotion of the field of insect behavior. A National Defense Education Act Fellowship and project allotment from the Agricultural Experiment Station, No. 603, made my graduate work possible.

I should also like to extend my appreciation to Dr. Hugh Dingle of the Department of Zoology at the University of Michigan for suggestions concerning correcting behavior of insects.

I am also indebted to my wife, Edith, for understanding, patience, and help throughout the preparation of this thesis.

LITERATURE CITED

Ballachey, E. L. and J. Buel. 1934.
    Centrifugal swing as a determinant of choice-point behavior in maze
    running of the white rat. J. Comp. Psychol. 17:201-223.

Dashiell, J. F. and A. G. Bayroff. 1931.
    A forward-going tendency in maze running. J. Comp. Psychol.
    12:77-94.

Dingle, H. 1961.
    Correcting behavior in boxelder bugs. Ecology. 42:207-211.

Glanzer, M. 1953.
    The role of stimulus satiation in spontaneous alternations.
    J. Exp. Psychol. 45:387-393.

Grosslight, J. H. and W. Ticknor. 1953.
    Variability and reactive inhibition in the mealworm as a function
    of determined turning sequences. J. Comp. Physiol. Psychol.
    46:35-38.

Grosslight, J. H. and P. C. Harrison. 1961.
    Variability of response in a determined turning sequence in the
    mealworm (Tenebrio molitor). An experimental test of alternate
    hypotheses. Animal Behavior. 9:100-103.

Hull, C. L. 1943.
    Principles of Behavior. New York: D. Appleton-Century Company,
    422 p.

Hullo, A. 1948.
    Role des tendances motrices et des données sensorielles dans
    l'apprentisage du labyrinthe par les blattes (Blatella germanica).
    Behavior. 1:297-310.

Lepley, W. M. and G. E. Rice Jr. 1952.
    Behavior variability in paramecium as a function of guided act
    sequences. J. Comp. Physiol. Psychol. 45:283-286.

Rice, G. E. Jr. and R. H. Lawless. 1957.
    Behavior variability and reaction inhibition in the maze behavior of
    Planaria dorotocephala. J. Comp. Physiol. Psychol. 50:105-108.

Schneirla, T. C. 1929.
    Learning and orientation in ants. Comp. Psychol. Monog. 6:1-142.

Sherrington, C. 1906.
    The Integrative Action of the Nervous System. New Haven: Yale
    University Press. 411 p.

Witkin, H. A. and T. C. Schneirla. 1937.
    Initial maze behavior as a function of maze design. J. Comp. Psychol.
    23:275-304.

Zeaman, D. and B. J. House. 1951.
    The growth and decay of reactive inhibition as measured by alternation
    behavior. J. Exp. Psychol. 41:177-186.

CORRECTING BEHAVIOR BY INSECTS
ON VERTICAL AND HORIZONTAL MAZES

by

ROGER DAVID AKRE

B. S., University of Minnesota, Duluth, 1960

———————————

AN ABSTRACT OF A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Entomology

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1962

This study concerns a phenomenon of behavior common to animals that are run in a maze with a 90° forced turn at the end of the starting runway. A short distance beyond the forced turn there is a choice point where one runway continues straight ahead and the other runway is parallel to, and away from, the starting runway. Animals which turn and follow the runway parallel with the starting runway are said to have "corrected" or exhibited correcting behavior (Dingle, 1961). This study attempted to determine factors affecting this behavior.

Both vertical and horizontal mazes were used for testing red milkweed beetles, Tetraopes tetraophthalmus (Forster), and a significant amount of correcting was found on all mazes. Factors which influenced the proportion of beetles correcting were investigated. Correcting behavior decreased markedly when the beetles were tested in the dark or with their eyes covered with black paint. Other factors which influenced correcting behavior were amputation of the antennae, the width of runway, length of the starting runway, distance from the forced turn to the choice point, and the length of time the beetles had been in the laboratory. One maze used with the milkweed beetles was designed to control thigmotactic stimuli and minimize centrifugal swing.

Yellow mealworms, Tenebrio molitor Linnaeus, were also found to show a highly significant amount of correcting. All the mazes used with mealworms were U-shaped grooves just wide enough for the larvae to fit into the runway. This design minimized thigmotactic stimuli and centrifugal swing. It was found that centrifugal swing could not be entirely controlled using either yellow mealworms or red milkweed beetles. At the forced turn the insects pressed their bodies much harder against the far wall of the forced turn and this enhanced the percentage of correcting.

Three major hypotheses have been suggested to explain this type of behavior in animals. They are: (1) successive induction (Sherrington, 1906); (2) centrifugal swing (Schneirla, 1929); and (3) reactive inhibition (Hull, 1943).

It was concluded that correcting behavior in mazes could best be explained by a combination of centrifugal swing and either one or both of the other concepts.

It is suggested that correcting behavior may result in some nonrandom distributions of insects on plants.