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MODIFICATION OF THE INNATE BEHAVIOR OF COCKROACHES ¹

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Four figures

Graber's ² experiments proved long ago that cockroaches, *Periplaneta orientalis* L, avoid the light and seek the dark. After having verified Graber's observations, I sought to change

FIGURE 1. Apparatus for study of the modifiability of reaction to light in the cockroach. a c, glass-box; d b, covered part of box; e and f, electrodes.

the direction of movement by teaching them, by means of the punishment method ³ to seek light and avoid darkness.

The apparatus used in these experiments is shown in Figure 1.

¹ The writer begs to acknowledge his indebtedness to Mr. Przibram, Director of the Institute for Experimental Biology in Vienna, for many helpful suggestions and criticisms.

² Graber, V. Grundlinien zur Erforschung des Helligkeits- und Farbensinnes des Tiere. Prag. 1884, S. 147-157.

³ Yerkes, R. M. The dancing mouse. New York. 1907, pp. 98-99.

The base of the apparatus is formed of 29 insulated copper plates, each 0.5 cm. wide. The distance between plates is 0.1 cm. The unpaired plates are connected with a long plate on the one side of the base and the paired plates with a *similar* plate on the other side. The two long plates are connected with an induction apparatus and this, in its turn with an accumulator of 2 volts. By this manner of setting up the current, all the non-paired plates form one electrode and all the paired ones a second electrode. Above the base is a bottomless glass box, (Fig. 1 ac) 19 cm. long, 2.7 cm. wide and 8.5 cm. high. Two-fifths of this box is entirely covered with black paper (Fig. 1 db).

In order to determine at first to what degree cockroaches are influenced by the electric shock, I removed the glass box and placed in its stead another bottomless glass box, 16 cm. square, in order to prevent the animal from escaping. I then put a cockroach into this second glass box and observed that after running about for some time the animal came to rest. I then turned the electric current upon it. I began with a very light shock (distance of coils being 19 cm.) and increased the intensity gradually. The first visible reaction set in at an average of 14.5 cm. distance of the induction coils. This reaction showed itself by the animal suddenly moving about, running to and fro and trying to crawl up the glass walls. The intensity of the current at 12-13 cm. distance of the coils seemed to be most effective, and this intensity was used in all subsequent experiments. A higher intensity caused temporary paralysis, if used for a time.

All the animals I experimented upon were male larvae,⁴ about one and a half years old, whose parents had been bred and kept in the Vienna Biological Institute.

During the definite experiments, and at the end of each series of experiments, the floor of the apparatus and the walls of the glass box were thoroughly cleansed with cotton wool moistened with alcohol in order to deodorize the apparatus.

After having replaced the covered glass box, Fig. 1, on the base, I started the definite experiments now to be described. (A cockroach was placed in the lighter part of the box; it imme-

⁴ Mature animals differ externally from old larvae only by the presence of the pair of rudimentary wings.

diately turned towards the darker part, which it entered. Thereupon I turned the current upon it. The animal, on receiving the electric shock, ran wildly about, tried to crawl up the walls, and then ran back to the light part. As soon as it had retreated to the lighter region, I switched off the circuit. After a short time, the cockroach again entered the darkened part and received another shock. When this procedure had been repeated a variable number of times, according to individual differences, the animal running in the direction from light to dark, on attaining the boundary line between the light and the dark, would suddenly stop, move its head and thorax in all directions and begin rapidly working with its antennae. After a time it usually turned back to the light. This behavior is, I think, the first stage in the overcoming of phototropism by training; untrained cockroaches do not behave in this manner. After a short time the animal would again return to the darkness, and again receive a shock. Its behavior now completely changed, for it no longer ran about in the dark region, but at once retreated towards the light. Having attained the boundary line between light and darkness, it turned towards the light. The number of turnings back from the boundary line between darkness and light into the light without receiving a shock increased with training. I considered the training complete when the animal, being in the light, turned back to the light ten times on arriving at the boundary line between light and darkness, without receiving a shock. All of the ten cockroaches used in my experiments succeeded in doing this.

During the experiments, when experience of the situation had already been gained, it repeatedly happened that an animal coming from the light to the boundary line between light and darkness, remained still of its own accord, with its head pointed towards the darkness. When I excited the animal to move by stroking its back (*dorsum*) by means of a strip of paper, it struggled against going into the darkness and turned towards the light in order to escape the irritating strip of paper. Table I shows the results of the experiments.

With the exception of Nos. 3 and 5, the cockroaches were tested at the same time of day, two o'clock in the afternoon, without intermission until they finally made the required number of turnings back. The time necessary for training was on

the average from three-quarters to one hour. The training of Nos. 3 and 5 could not be finished on the same day because of the great fatigue from which they suffered. As the table shows, there are very great differences in their modes of learning.

TABLE I
REACTIONS OF COCKROACHES TO ELECTRIC SHOCK WHEN MOVING TOWARD
A DARK BOX

Number of animal	Number of shocks	Number of turnings back	Number of animal	Number of shocks	Number of turnings back
1	5	1	4	115	4
	12	5		116	10
	15	4			
	16	5		7	2
	17	5		8	1
	18	1		9	1
	20	1		10	3
	21	5		11	1
	22	1		12	4
	25	3		13	8
	27	2		14	1
	31	3		15	7
	32	2		16	10
	33	1			
	36	2		30	3
	37	10		32	1
				37	2
	6	1		38	2
2	7	1		40	2
	23	1		43	4
	24	2		44	2
	28	10		45	6
			5	46	3
	11	1		61	2
	13	2		70	1
	21	1		(pause of 1 day)	
	22	1		87	1
	41	1		88	6
	42	1		94	5
	52	1		95	6
	58	6		96	10
3	64	5			
	65	3		12	1
	67	2		19	2
	68	2		23	2
	69	1		27	1
	70	1	6	35	3
	71	1		37	1
	87	1		41	8
	(pause of 2 days)			42	5
	106	3		43	1
	107	4		44	10
	112	1			
	113	1		19	3
	114	7		20	1

TABLE I—*Continued*

Number of animal	Number of shocks	Number of turnings back	Number of animal	Number of shocks	Number of turnings back
7	22	1		29	8
	25	2		37	10
	27	1			
	31	6		10	2
	32	10		12	1
				23	1
				37	1
	6	4		39	3
	7	2		49	4
	12	1		50	2
8	13	4	10	55	5
	14	4		56	1
	15	6		58	1
	17	8		63	1
	21	4		68	5
	22	2		82	1
	23	10		93	2
				94	1
				95	9
	8	1		100	3
9	12	3		105	1
	14	6		109	1
	22	6		112	6
	23	2		114	1
	28	4		118	10

While 16 shocks were sufficient for No. 4, No. 10 performed the ten obligatory turnings back only after having received 118 shocks. It may therefore be assumed from the different manners of learning that there were three types of cockroaches.

Let us mark the curves of learning based upon the results gained with the ten cockroaches. In all the curves, abscissas represent the number of shocks; and ordinates the number of the turnings back without receiving a new shock. Figure 2 shows the curves of Nos. 2, 4, 6, 7 and 8; Figure 3, those of Nos. 1 and 9; Figure 4, those of Nos. 3, 5 and 10.

The curves of the first series (Fig. 2) are similar in character, since they ascend successively till the crest is attained. The number of shocks necessary for producing the definite result is rather small. These data, however, prove that after the first experience of the shock, the animals made continuous progress. Thus the curves show no important or prolonged failure.

Fig. 4 represents the curve of the third series. This curve is much longer and shows that the animals learn only after

having received many shocks. Perfection was gained only after a long time, but the fact that the curves Nos. 3 and 5 show two crests is particularly interesting. The one is a definite one, the other takes place about the middle of the course of the curves. The curve for No. 10 presents three crests. While the interest of the crests consists in their showing the progress of the learning, the space between the crests may be considered as the consequence of fatigue. I noticed external signs of fatigue, in all the cockroaches referred to, after the first crest had been attained. The animal remained motionless on the

FIGURE 2. Representation of the reactions of cockroaches Nos. 2, 4, 6, 7, and 8. Number of turnings from dark box indicated on axis of ordinates. Number of electric shocks indicated on axis of abscissas.

same spot or when excited to movement shot blindly along the walls, failing to stop on the boundary line between light and darkness. In the same way, the movements of the thorax and the antennae, previously described, ceased when the animal had arrived at the boundary line. The effect of the electric shocks upon the animal seemed to be lessened. As soon as the animals had rested, they were able to attain the second crest and the experiments were completed.

The tests of No. 10 were achieved in the same trial, those of No. 3 after the elapse of one day, and those of No. 5 after two days. Thus the two elements of these curves, crests and

failures, refer to two factors concerned in the process of learning: *practice* and *fatigue*.

The curves of the second series (Fig. 3) resemble those just described in that they also show two crests. The difference consists in the small number of shocks necessary to obtain definite results of learning. This circumstance, however, brings it near to the curves of the first series. Thus the curves of the second series take an intermediate position between the two others.

FIGURE 3 Representation of the reactions of cockroaches Nos. 1 and 9.

The results of an analysis of the curves enables us to separate the cockroaches tested with respect to their ability in learning, into three groups as shown in the following table.

	Characteristics of the curve	Characteristic features of the cockroaches in learning
1	{ Short One crest	Rapid progress with practice Slow fatigue
2	{ Short Two crests	Rapid progress with practice Rapid fatigue
3	{ Very long Two crests	Slow progress with practice Rapid fatigue

The analysis of the curves and the possibility of isolating two factors, *practice* and *fatigue*, permit us to assert that the learning-curves of cockroaches may be considered a special case of Kraepelin's "Arbeitscurve."⁵

⁵ Kraepelin. Die Arbeitscurve. Phil. Studien, 1902, Bd. 19. S. 459-507.

FIGURE 4. Representation of the reactions of cockroaches Nos. 3, 5, and 10, and of the re-learning reactions (R L) of No. 10.

Marked individual differences were noted with respect to the time during which the cockroaches retained their newly acquired habit.

The data given below were gathered by measuring the time elapsing between the last effective shock given and the animal's retreat into the dark part of the glass box.

TABLE II

No. of animal	Time of permanent avoiding of the dark
3	3' 53"
9	10' 57"
4	11' 20"
8	11' 48"
5	13' 3"
2	14' 24"
7	18' 32"
10	25' 15"
6	55' 0"

No relation is evident between the degree of permanency of the newly acquired habit and the number of shocks necessary to establish it. Though the training influences the behavior of the cockroaches only for a short time, the memory of it lies latent, as is proved by the rapidity with which they relearn. An animal once trained after a few days performs the obligatory number of turnings-back after only a few shocks have been applied. The following table shows the results of relearning

TABLE III

No. of animal	Number of shocks necessary for learning	Number of days between learning and relearning	Number of shocks necessary for relearning
10	118	1	17
9	37	2	12
8	23	3	4
4	16	6	5
1	37	9	7

The curves of relearning resemble those of the first series. They indicate rapid progress without noteworthy fatigue. As an example of the curve of relearning, I give that for No. 10, Fig. 4, R L, 10.

Before concluding my description of the experiments, I must mention that it was possible to establish the habit in an animal whose antennae had previously been removed. A hundred and twenty-six shocks were required before the animal performed

the obligatory ten reversals. The learning-curve is the same as those of the third series in normal animals.

Felix Plateau ⁶ has recently stated, as a general conclusion drawn from his experiments with bumblebees, that "chez Bourdous et vrais-semblablement chez les autres insectes la mémoire des faits n'existe pas" (p. 159). The results of my experiments do not support this statement.

⁶ Plateau, F. Les insectes ont-ils la mémoire des faits? *L'année psychologique* 1909, t. 15. pp. 148-159.