OLFACTORY AND VISUAL LEARNING IN THE RED-EARED TERRAPIN, *PSEUDEMYS SCRIPTA ELEGANS* (WIED.)

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INTRODUCTION

The possible olfactory functions of the mammalian forebrain, particularly of the 'rhinencephalon' have been studied by a number of workers (Allen, 1940; Swann, 1934; Lashley & Sperry, 1943; Brodal, 1947; Cragg, 1960). The view that the mammalian rhinencephalon might play an important part in olfaction was originally based upon the evidence of comparative anatomy and it was therefore of interest to develop a method for studying olfactory behaviour in a reptile. A chelonian was chosen for the present investigation because Chelonia have a well-developed olfactory apparatus and because the central olfactory connexions are similar in general to those found in amphibians and mammals (Goldby & Gamble, 1957).

A number of training experiments on chelonians are to be found in the literature. Only a few are concerned with olfaction but it has been thought useful to give a more complete list of training experiments here.

Yerkes (1901) appears to have been the first to train a chelonian. He showed that *Chelopus* could learn a simple maze, and Tinklepaugh (1932) showed the same for *Clemmys*. Seidman (1949) compared the learning of a direction habit in a T maze by *Pseudemys* and a newt *Triturus*, and found that the terrapin could reverse the habit more readily than the newt. More recently Kirk & Bitterman (1963) have studied reversal in a T maze using *Chrysemys*. Eskin & Bitterman (1961) and Gonzalez & Bitterman (1962) have investigated partial reinforcement in *Pseudemys* and *Chrysemys*. Humphrey (1933) has described habituation in *Testudo*.

Casteel (1911) used a Yerkes box to demonstrate light-intensity discrimination and fairly complex form discriminations in *Chrysemys*. Kuroda (1933) using a similar method demonstrated a number of simpler form discriminations in *Clemmys*, and Wojtusiak (1933, 1934), Bartowiak (1949) and Mlynarski (1951) have demonstrated form and colour discrimination in *Emys*, *Clemmys* and *Geoclemmys*. Wojtusiak (1947) and Wojtusiak & Mlynarski (1949) demonstrated infra-red vision in *Emys*, and Dudziak (1955) has used a training technique to determine the visual acuity of *Emys* in air and water. Quaranta (1952) has confirmed some of the work of Wojtusiak and his school. He was able to train giant tortoises from Galapagos and the Indian Ocean to discriminate between chromatic pairs of blue, green and red. Fischel (1934) in *Chelydra* apparently obtained evidence of insight learning.

Auditory discriminations have been claimed by Andrews (1915) and Poliakov (1930) in two species of *Chrysemys* and *Emys*, but Kuroda (1923, 1925) could not confirm Andrews's experiments while using *Clemmys*.

There is no published information as to the innate responses of *Chelonia* to olfactory stimuli. Allard (1949) could find no certain differential responses by *Terrapene* to fish and stones wrapped in burlap bags. And we have discovered no innate olfactory responses during this work.

Parschin (1929), Poliakov (1930) and Alexanyan & Asratyan (Asratyan, 1953) have used conditioned-reflex techniques to study a variety of sensory modalities in chelonians. Poliakov included olfactory conditioning in his experiments. He used amyl acetate, turpentine, camphor and clove oil in a study of three animals. The animals were able to differentiate the four substances that he used and needed about 300 trials to establish a conditioned reflex, which became steady after a further 300 trials. Asratyan (1953) was able to produce conditioning to mechanical stimuli after twenty couplings or less. He also produced conditioned responses in decerebrate animals. His method has been tried on the present animals but with only very limited success.

MATERIALS AND METHODS

The red-eared terrapin, *Pseudemys scripta elegans* (Wied.) was used for these experiments (Carr, 1952). The animals were obtained from American and English dealers and varied in age from about 2 months to 2 or 3 years old as estimated from the data of Cagle (1946). Details of the care of these animals are given by Boycott & Robins (1961).

Operations and histology

The animals were anaesthetized with ethyl ether. Induction took half an hour or more but recovery was usually rapid and the animals fed within 24 hr. Most of the lesions were made in the olfactory fibres where they enter the bulb. The skull was opened with a dental burr and the lesion was made with a heated platinum wire. The wound was closed with gelatin sponge and sealed with 5 % celloidin.

The animals were killed with 5–10 ml. of 5 % urethane injected intraperitoneally. Some of the heads were fixed in Nonidez fixative (Nonidez, 1939), and the relevant part of the brain was then dissected free and stained by the Nonidez method. Other heads were fixed in formol saline, decalcified in nitric acid, double embedded and the serial sections were stained with the Holmes silver method (Holmes, 1947), haematoxylin and eosin, or acid fuchsin.

Training

The following method has been found useful for training terrapins to discriminate a number of stimuli. It was designed primarily for testing olfactory* stimuli and this placed certain limitations on the design. The smells had to be completely cleared between trials. Because the animals are air-breathers, they had to be given time to sample the air and water, and the situation was designed so that the animals would not be required to localize the smells. Early experiments in which some localization was demanded were unsuccessful. The method has been found suitable for visual and gustatory stimuli as well.

The experimental tank was the same size as the home tank, 2 ft. × 2 ft. × 1 ft. A

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* The term 'olfactory stimulus' has been used in the present context to refer to any stimulus that reaches the central nervous system via the olfactory nerves. Stimuli that reach the nervous system over other paths are classified as taste or general chemical sensation. Hasler (1954) has used the same classification for his fish experiments.

sheet of stainless steel 2 in. high and 1 ft. 10 in. long was placed down each side of the tank. The tank was filled with tap water up to the top of the steel and the two steel sheets were connected to the output of a 'Variac' transformer to give a shock which was found sufficient to produce retraction of the head and to deter the animal from feeding. The shock was 60 V. 50 cyc. a.c. For a discussion of the current flowing through the animals under such conditions see Mrosovsky (1964).

Two kinds of trial were given. 'Positive' trials, in which the animals were allowed to feed and 'negative' trials, in which they were not allowed to feed but were given a shock as soon as they snapped at the meat. For each trial three or four pieces of chopped lamb's heart were placed at one end of the tank and a few millilitres of tap water (positive trials) or supposed olfactory stimulant (negative trials) were allowed to diffuse throughout the tank. For all trials the animals were placed in the training tank for 60 sec. but any that received a shock were then removed. The shocks were of 1–2 sec. duration. In recent experiments a timing device giving a shock lasting exactly 2 sec. has been used.

The trials had to be spaced to allow the smell to be completely washed out between trials and this limited the number of trials that could be given each day. Early experiments suggested that four single trials spaced 2 hr. apart gave too slow a rate of learning. For this reason four pairs of trials were given each day, two positive pairs and two negative pairs. The trials in each pair were about 5–10 min. apart. The positive and negative pairs were presented in random order, with the limitation that there had to be two pairs of each kind each day. There was a 2 hr. interval between successive pairs of trials during which the tanks were washed with continuously running water.

Trials were run for 5 days each week, and the scores have been given as the total number of correct responses (feeding in positive trials, not attempting to feed in negative trials), in each week. The second trial of each pair helped to establish and maintain the discrimination but was not used in the final scoring, since factors other than olfactory clues are likely to enter into the second trials. Thus scores for second trials tend to be slightly higher than scores for first trials, particularly during the early stages of training. Only the first trial of each pair has been scored in the following account.

During the early stages of training after they had received a few shocks, many of the animals showed cautious behaviour characterized by approaching the meat with the head retracted and the hind limbs extended; slow approach to and rapid retreat from the meat; snapping several inches short of the meat; and swimming into the meat without snapping at it. Such behaviour occurred in the early negative and a few of the positive trials and disappeared in both situations as learning progressed.

Before training in the discrimination animals were given two pairs of positive trials only each day. This 'habituation'* was scored on the basis of first trials only and the scores are, therefore, out of 10. During training the animals were allowed to feed in positive trials and were otherwise only fed at the end of the day on the diet described by Boycott & Robins (1961).

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* Habituation is used to refer to a series of positive trials only. During a period of habituation the fright responses that animals show when they are handled wane: there is also a 'positive' training which shows as an increased readiness to swim from one end of the tank to the other, and to feed.

RESULTS

A. *Early experiments with amyl acetate*

Table 1 shows the scores of twelve animals that were given shocks in the presence of amyl acetate. 1 ml. of amyl acetate was put in the tank for the first trial of each pair, and a further ½ ml. was added for the second trial. Of these animals only animal 99 showed no discrimination. In these early experiments a number of animals were lost on account of disease (see Boycott & Robins, 1961) and only five animals could be used for making olfactory lesions. The animals were rehabituated postoperatively and Table 2 shows their postoperative training scores.

Table 1. *Amyl acetate discrimination in terrapins with no olfactory lesions*

Animal no. ...	70	72	74	99	100	105	108	115	116	117	118	119
Week no.												
1	7/8	7/8	3/8	7	10	9	6	3/4	4/4	3/4	4/4	4/4
2	10	9	8	8	10	10	8	10	10	10	10	10
3	11	11	12	7	11	10	8	10	10	8	10	10
4	15	14	17	11	13	11	10	11	12	10	11	10
5	14	18	14	9	16	15	8	15	12	12	12	11
6	X	X	X	12	17	15	13	16	16	14	18	12
7	18	18	15	8	20	12	13	15	17	12	13	12
8	—	—	—	—	—	18	16	12	15	15	10	16
9	—	—	—	—	—	17	19	12	18	13	13	17
10	—	—	—	—	—	20	18	14	14	16	14	18
11	—	—	—	—	—	—	—	14	15	16	13	16
12	—	—	—	—	—	—	—	X	X	X	X	X
13	—	—	—	—	—	—	—	14	12	13	16	18
14	—	—	—	—	—	—	—	14	†	13	16	13

Notes: Each figure gives the number of correct responses in the first trials of the pairs. The figures above the line give habituation, below the line training. Where less than ten pairs of trials (habituation) or twenty pairs of trials (training) were given the score is shown as a proportion of the total number of first trials. X: 9 days without trials, †, Animal died.

Table 2. *Amyl acetate discrimination in terrapins with olfactory lesions*

(For preoperative scores see Table 1. Notes as for Table 1.)

Animal no. ...	70	72	74	105	108
Week no. (post-operative)					
1	5/6 / 5/8	4/6 / 4/8	0/6 / 4/8	6/8	3/8
2	10	10	10	10	10
3	9	9	11	14	13
4	13	8	10	15	13
5	—	—	12	13	17
6	—	—	12	16	9
7	—	—	9	14	11
8	—	—	—	†	12
9	—	—	—	—	†

In a second group of animals similar lesions were made without any preoperative training. The animals were habituated postoperatively and subsequently gave th(

scores shown in Table 3. Of the animals shown in Table 2 and 3 only 71, 73, 75, 101, 102 and 105 showed clear signs of discrimination. Table 4 summarizes the lesions as checked on the serial sections. In this table the animals are grouped according to their postoperative performance to facilitate comparisons.

Table 3. *Amyl acetate discrimination in terrapins with olfactory lesions*

(No preoperative training was given. Notes as for Table 1.)

Animal no. ...	71	73	75	101	102	120	121	122
Week no. (post-operative)								
1	7/8	8/8	8/8	7/8	6/8	6/8	3/8	4/8
2	10	10	5	9	10	9	9	10
3	10	10	10	8	12	9	9	10
4	7/12	7/12	10/12	8	13	10	9	10
5	17	14	16	10	15	10	11	9
6	17	17	17	12	15	11	12	11
7	17	17	19	15	15	10	11	11
8	—	—	—	14	19	12	7	13
9	—	—	—	15	—	10	11	†
10	—	—	—	19	—	10	9	—
11	—	—	—	17	—	—	—	—

Table 4. *Olfactory lesions in terrapins shown in Tables 2 and 3*

Animal no.	Description of lesions
75	Scar in ¼ to ½ of the fibres
71	Scar in less than ¼ of the fibres
73	Scar in ¼ to ½ of the fibres
105	Scar in ¼ of the fibres
102	Scar in less than ¼ of the fibres
101	Scar in over ½ of the fibres
108	Complete lesion
70	Complete lesion
72	Scar in ¾ of the fibres
74	Scar in over ¾ of the fibres
102	Complete lesion
121	Complete lesion
122	Complete lesion

There appears to be an inverse relationship between the extent of the lesion and the postoperative score. The high early scores given by 108 are the only exception. It is possible that this animal had an incomplete lesion that was later extended by secondary vascular damage, but other than the worsening of performance this animal showed no noteworthy change between the third and fourth week. Of the animals that showed postoperative discrimination 101 had the largest lesion. It is of interest that the discrimination only appeared after about 5 weeks (see p. 575).

The animals with incomplete lesions show that the operative trauma does not interfere with the discrimination. The loss of discrimination is produced specifically by damage to the olfactory fibres. Also, since the extent of the lesions was not known until the sections were examined (and the early incomplete lesions were a surprise to us) the possibility that unconscious clues were given during training can be excluded.

From these preliminary experiments it can be concluded that the red-eared terrapin can detect amyl acetate and that this ability is lost after destruction of more than half of the olfactory fibres.

B. *Other preliminary experiments*

Animals 65, 66 and 67 were trained using 50 ml. of 1% vanillin (although the amounts were smaller in the early parts of the experiment). Table 5 shows that a discrimination was established in these animals. Only 65 and 66 survived the operation in which the olfactory fibres were cut anterior to the bulb. Animal 65 gave scores of 9, 7, 8, 13, 13, 11, 11 in the seven weeks after operation. Animal 66, which did not attack for 2 weeks after the operation, was finally rehabituated and was then run for 2 weeks scoring 8 and 10. The lesion in 65 was complete. In 66 approximately half of the olfactory fibres had been cut.

A similar experiment, using 1 ml. of eucalyptus oil was carried out with animals 50, 51 and 56. Table 5 shows that these animals learned the discrimination. The olfactory lesions were unsuccessful.

Table 5. *Vanillin and eucalyptus discrimination in terrapins with no olfactory lesions*

(Arrows indicate when amount of vanillin was increased; other notes as Table 1.)

	Vanillin				Eucalyptus		
Animal no.	65	66	67		50	51	56
Week no.				Week no.			
1	12/12	12/12	12/12	1	17	20	14/20
2	4/4	4/4	4/4	2	20	20	13/24
	7/15	7/15	7/15	3	20	20	X
3	12	10	10	4	16/25	13/25	11
4	14	11	10	5	20/23	21/23	13
5	17	10	10	6	19/19	17/19	16
6	17	16	16	7	6/7	6/7	17
7	15	14	15	8	—	—	15/16
8	X	X	X	9	—	—	9/10
9	14	14	12		—	—	—
10	13	15	14		—	—	—

C. *Further experiments with amyl acetate and experiments with visual stimuli*

After the experiments of sections A and B had been completed it was found possible to improve the health of the animals kept in the laboratory (see Boycott & Robins, 1961) and a second group of animals was used to confirm and extend the above results. The results of sections A and B are marred by differing survival times, and they leave open the question whether destruction of the olfactory fibres interferes with olfactory learning only, or whether it may have a more general effect on learning in the present situation. The following experiment was designed to answer this question. The results are given in Table 6, which shows that olfactory lesions interfere with amyl acetate discriminations but do not affect visual discriminations.

Twelve animals were habituated and of these one failed to feed more than two or three times during 6 weeks' testing. Of the remaining eleven animals six were trained to amyl acetate ('olfactory animals') and five to a visual discrimination ('visual

animals'). The procedure during the visual training was the same as for the olfactory training except that in the negative trials a strip of black Perspex (2 in. × 11 in. and supported by a 1 in. horizontal piece) was placed across the whole of one end of the tank.

Table 6. *Amyl acetate and visual discrimination in terrapins*

	Amyl acetate							Visual					
Animal no.	150	152	154	156	158	160		151	153	155	157	159	
Week no.							Mean						Mean
1	8	6	6	3	10	10	7·2	8	7	6	10	7	7·6
2	10	9	10	8	10	10	9·5	10	10	10	10	10	10·0
3	11	12	10	13	16	15	12·8	17	16	14	15	16	15·6
4	13	15	13	18	14	19	15·3	20	17	19	19	19	18·8
5	18	19	14	17	14	17	16·5	20	15	19	16	19	17·8
6	17	20	17	19	20	19	18·7	20	16	20	20	17	18·6
7	18	18	14	18	19	19	17·7	19	14	20	19	19	18·2
8	19	15	13	18	20	18	17·2	20	16	19	20	20	19·0
				Lesions to olfactory fibres									
9	9	6	6	1	6	4	5·3	9	10	10	10	10	9·8
10	10	8	10	7	10	9	9·0	10	10	10	10	10	10·0
11	10	10	10	9	10	10	9·8	10	10	10	10	9	9·8
12	11	13	9	11	13	14	11·8	20	19	20	20	20	19·8
13	10	15	12	8	14	13	12·0	20	20	20	20	20	20·0
14	10	12	9	10	11	15	11·2	20	20	20	19	19	19·6
15	11	12	9	10	10	17	11·5	20	19	20	20	19	19·6
16	14	10	10	11	14	16	12·5	20	17	20	20	20	19·4
17	11	10	11	11	11	16	11·7	20	18	20	20	19	19·4
18	13	16	11	13	13	15	13·5	—	—	—	20	19	—
19	13	17	12	12	12	10	12·7	—	—	—	19	20	—
20	17	16	13	17	13	18	15·7	—	—	—	20	19	—
21	15	12	13	17	16	16	14·8	—	—	—	19	19	—
22	19	11	15	17	16	18	16·0	—	—	—	20	20	—
23	12	14	18	15	15	15	14·8	—	—	—	19	20	—
24	15	19	20	15	14	16	16·5	—	—	—	20	19	—
25	15	17	18	16	17	19	17·0	—	—	—	20	20	—
26	16	15	19	18	17	16	16·8	—	—	—	19	19	—
27	17	19	19	18	14	14	16·8	—	—	—	20	20	—

Notes as for Table 1. As the performance of the visual animals was so consistent only 157 and 159 were continued until the end of the experiment.

All eleven animals were feeding regularly in the training tank at the end of 2 weeks, and all had clearly learned the discrimination after 4 weeks of training (Figure 1). The results show that the visual situation is learned more readily than the olfactory situation. At test with 5 degrees of freedom = 3·0; $P < 0·05$.

At the end of 6 weeks training all the animals had lesions made in the olfactory fibres at their entrance to the bulb. Some of the lesions also damaged a small portion of the anterior part of the bulb. Habituation was started on the following Monday and during the first week after operation an interesting difference appeared between the two groups of animals. The olfactory animals fed much less frequently than did the visual animals, and when they did they were usually slower. Table 7 shows the daily scores, including first and second trials, during the first post-operative week. The differences between the scores obtained during the first 3 days of this week are striking. Whereas the visual animals attacked in 59 out of 60 trials, the olfactory

animals only attacked in 37 out of 72 trials. Both groups fed readily in the home tank at the end of the day. This failure to attack is presumably the direct result of removing the clues which the olfactory animals use to decide whether or not to attack. The effect had worn off considerably by the second week and there was no difference between the two groups in the third week.

At week 12 training was begun again. During the next 6 weeks the visual animals performed with a high degree of accuracy and this was maintained for a further 10
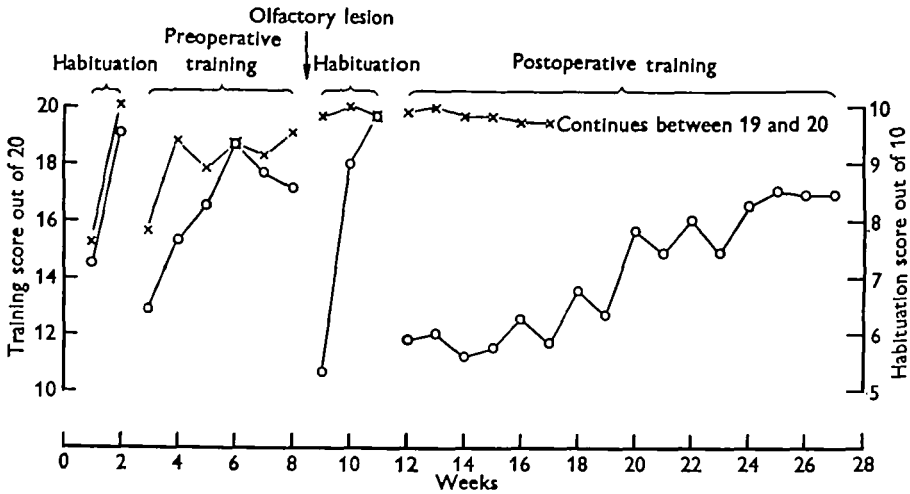
Fig. 1. Weekly scores of the animals 150–160 (see Table 6). The means for the olfactory animals are shown: O—O. Those for the visual animals: × — ×. The training scale showing the score out of 20 is given on the left. The habituation scale showing the score out of 10 is given on the right (see p. 569).

Table 7. *Daily scores of terrapins* 150–160 *during first week after operation* (*week* 9, *Table* 6).

(Total of first and second trials.)

Animal no.	Olfactory training						Visual training				
	150	152	154	156	158	160	151	153	155	157	159
Day											
1	4	1	0	1	0	2	3	4	4	4	4
2	2	1	3	2	1	3	4	4	4	4	4
3	4	4	3	2	1	3	4	4	4	4	4
4	3	4	4	1	3	3	4	4	4	4	4
5	4	4	4	3	4	3	4	4	4	4	4

weeks in animals 157 and 159. The table shows that there was full retention during the 3 weeks in which no negative trials were given. The olfactory animals during weeks 12 to 17 gave lower scores than those given by the visual animals, and also lower than those given by the same olfactory animals preoperatively. The olfactory lesions thus had a specific effect upon the original amyl acetate discrimination, which must, therefore, depend upon the olfactory nerves to a large extent (fig. 1).

However, the scores were more often above 10 than would be expected on random

performance and by week 20 there was clear evidence of discrimination. During the weeks 22–27 the performance reached preoperative levels. Comparing the last 3 weeks of the preoperative performance with the last three postoperative weeks, the preoperative scores were 321/360 and the postoperative 304/360. This recovery of the discrimination could be due to an ability to detect amyl acetate through the taste buds or general chemical receptors; or it could be the effect of incomplete lesions. It is also possible that some regeneration of the olfactory nerve fibres had occurred. There was no obvious histological evidence of regeneration in these experiments but since these fibres are extremely fine, regeneration would be difficult to detect. The histological material showed that none of the lesions was complete (see Table 8). Comparison of Table 8 with the postoperative performance (Table 6) does not show that the size of the lesion is clearly related to postoperative discrimination when $\frac{1}{2}$ or more of the fibres are destroyed (p. 571). Only animal 160 whose postoperative performance is better than that of the rest of the olfactory animals shows some such relation. This animal had the smallest lesion. It has, however, been included in the above figures and in Fig. 1.

Table 8. *Olfactory lesions in terrapins 150–160*

Animal no.	Description of lesions
	Olfactory training
150	Scar in $\frac{1}{4}$ of the fibres
152 154 156 158	Scar in $\frac{3}{4}$ of the fibres
160	Scar in $\frac{1}{4}$ of the fibres
	Visual training
151	Scar in $\frac{3}{4}$ of the fibres
153 155	Scar in $\frac{1}{4}$ of the fibres
157	Scar in $\frac{3}{4}$ of the fibres
159	Very slight, insignificant, scarring of the fibres

The possibility that terrapins can also discriminate amyl acetate on the basis of taste cannot therefore be excluded. A few animals that were trained to citric acid showed that taste discrimination can be established using the present procedure.

DISCUSSION

These experiments show that terrapins can be trained to respond differentially to olfactory and visual stimuli and suggest that the same is true of gustatory responses. Since almost all the animals which were trained gave higher scores during the second and third weeks it can be concluded that we are dealing with a learned response rather than with an innate preference for the positive situation. If there were such an innate preference one would expect animals to take longer over an attack when they were first introduced to the negative situation. However, for the animals trained to amyl acetate the mean time for attack in the last habituation trial was 16·4 sec. (18 animals), while the mean time in the first negative trial was 14·9 sec.

In each group of animals a few were found which could not be habituated and these were rejected at the beginning of the experiments. Other authors, e.g. Casteel (1911) and Asratyan (1953), have had similar experience. The animals thus do not represent a random sample of the terrapin population available through dealers. In the experiments reported here it was necessary to reject about 10–15 % of the animals purchased. However, recently, of a group of forty-eight animals that arrived with the caruncle in place, only nine were sufficiently habituated for training to be started after 6 weeks. A further six were habituated after about 12 weeks. These animals all appeared to be healthy in that they fed and grew in the home tank for more than a year. Attempts to discover the basis of this high variability were unsuccessful, but it is important to emphasize that the results reported here are from animals selected on the basis of their habituation performance and that this can be highly variable.

SUMMARY

1. Terrapins have been trained to olfactory and visual stimuli. The animals are able to discriminate meat alone from meat with amyl acetate, vanillin, eucalyptus or a black figure.

2. The olfactory discrimination is learned less readily than the visual discrimination under comparable conditions.

3. Destruction of the olfactory nerves shows that amyl acetate and vanillin are olfactory stimuli. The discrimination to amyl acetate is lost for about 6 weeks after destruction of more than half of the olfactory nerves, and the postoperative feeding behaviour is temporarily altered.

4. Olfactory lesions do not disturb the discrimination or feeding behaviour of animals trained to a visual situation.

5. Animals with large olfactory lesions show recovery of the amyl acetate discrimination after 6 and more weeks of postoperative training. It remains to be determined whether the recovery is due to a taste or general chemical discrimination or to surviving olfactory fibres.

6. The method should prove suitable for studying the olfactory and perhaps other functions of the chelonian forebrain.

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