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THE DYNAMICS OF LEARNING IN THE PRAYING MANTIS (*STAGMATOPTERA BIOCELLATA*)

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Abstract—(1) A praying mantis faced with a bird displays a 'frightening reaction' called a deimatic reaction, habituation of this response is the learning process under study.

(2) Speed of learning and retention when the same number of training sessions are given, seem to depend only on the total number of trials per session.

(3) Anoxia with nitrogen during training, impairs retention on the following day, but this amnesic effect diminishes with training. After 8 days of training, memory proves to be insensitive to a N_2-shock.

(4) Mantis that receive two sessions of discontinuous training (30 trials/day each of 2 min duration with 10 min between trials) show long retention (at least 6 days) but this long memory is dramatically disrupted by N_2-anoxia.

(5) Results seem not to fit basic assumptions of the dualistic theory of memory, i.e. the STM–LTM dichotomy. It is suggested that the learning process involves two mechanisms with different physiological bases but which nevertheless act together during several training sessions. One mechanism would underlie memories that are sensitive to anoxia (S memory) and the other, memories that are insensitive (I memory). The relative participation of these mechanisms could change during training, in such a way that the greater the degree of training, the smaller the contribution by the S process and the greater that of I process.

(6) When mantis are trained with successive sessions each consisting of a single long trial of 2 hr per day (continuous training), they learn more slowly than when trained with the usual discontinuous method. With continuous training 10 sessions yield a level of habituation similar to that reached after 8 days of discontinuous training. However, after 10 days of continuous training, memory is still sensitive to impairment by anoxia. The possible meaning of this difference is discussed.

INTRODUCTION

A PRAYING mantis (*Stagmatoptera biocellata*) faced with a bird displays a 'frightening reaction' called a deimatic reaction, DR (MALDONADO, 1970). Habituation of this response due to repeated presentation of different species of birds has been studied (no-DR learning, BALDERRAMA and MALDONADO, 1971). These authors reported that when mantis are shown Java sparrows (*Padda oryzivora*) 30 times a day, a clear-cut decrease in the number of DRs is seen during 2 days of training and good retention is found after 6 days of rest interval. This waning of the DRs was demonstrated to fulfill the parametric characteristics of habituation (THOMPSON and SPENCER, 1966).

A closer analysis of the dynamics of this learning process is attempted in the present paper. The following aspects are examined:

(a) Relationship of the speed of learning and degree of retention to total time of training and total number of events, respectively.

(b) Influence of inter-trial spacing on the time course of no-DR learning. MALDONADO (1972) presented preliminary results showing that when mantis received only one trial of 2 hr per day, no fading of the response could be detected until after two days of training, in spite of the fact that animals continuously display the DR during the long trial. This finding is not surprising, since it has been known for a long time that massed training is less effective than distributed events (EBBINGHAUS, 1885; FOPPA, 1968). Similarly, ERBER (1975a,b), studying the dynamics of a learning process in the honey bee, found that rewards lasting longer than 1 min do not improve the performance. However, experiments with another type of learning in mantids, i.e. learning not to attack a mobile star (MALDONADO and TABLANTE, 1975), showed that the duration of the intertrial intervals has no influence on this learning process.

(c) Susceptibility to impairment by amnesic agents and memory consolidation. Since we are dealing with an effective but slow learning process, it would be expected that after 2 days of training, sufficient to assure good retention for 6 days (BALDERRAMA and MALDONADO, 1971), memories would resist disruption by amnesic agents. However, this expectation is based on the generally accepted idea that long retention implies a consolidated memory, and current experiments imply that this need not always be the case.

MATERIALS AND METHODS

Animals. The animals were adult *Stagmatoptera biocellata* that had reached maturity 20–30 days before the experiments. All animals had been reared in individual cages at a constant temperature of 29°C during the day and 24°C at night, with a relative humidity of 65% and 12 hr of light per day. They were fed with *Sarcophaga* flies at 4-day intervals.

Apparatus. The apparatus for no-DR training has been described elsewhere (BALDERRAMA and MALDONADO, 1971). Mantis were placed in individual cages (14 × 10 × 10 cm) with gauze net walls, except for the front one which was made of transparent celluloid. Each cage was put into one compartment (20 × 20 × 30 cm.) facing an opaque sliding screen. A bird (*Padda oryzivora* or *Molothrus bonariensis*) was enclosed in another cage with a front wall of transparent Lucite. Each bird-cage faced the sliding screen of the mantis compartment. Both compartments could be illuminated by fluorescent tubes. The set-up could accomodate 12 mantis and 12 birds at a time. During a trial the opaque sliding screens were elevated for 2 min (discontinuous training) or for 2 hr (continuous training). The deimatic reaction (DR) of the mantis during a trial was observed by the experimenter through the bird cage.

Training procedures. Two methods of training were used, discontinuous and continuous. (a) The discontinuous procedure was similar to that used in previous experiments (BALDERRAMA and MALDONADO, 1971). One training session (e_n) consisted of 5, 15 or 30 trials a day, each trial lasting 2 min with inter-trial intervals of 10, 23 or 85 min. The interval between sessions was 1 day. DRs were classified into five ranks, i.e. complete reaction (C): when mantis displayed the DR with all its components (MALDONADO, 1970) during the entire trial; incomplete reaction (I): when the reaction lasted throughout the trial but some of the components were absent; minus complete reaction (−C): when the C was not sustained for the full 2 min; minus incomplete reaction (−I): when the I was not sustained; and no-DR: when the mantis did not display any component of the DR during the trial. In order to assess the performance quantitatively, a value was assigned to each one of these five categories. Four points for C, 3 for −C, 2 for I, 1 for −I and 0 points for no-DR. (b) The continuous procedure, One training session (e_n) consisted of only one trial of 120 min. The total time during which a mantis was displaying a complete DR was recorded.

Sessions with both the discontinuous and continuous procedures started at 8 a.m.

Anoxia. In order to subject a mantis to anoxia, it was removed from its cage, and placed in a container through which a current of N_2 was passed for a period of 3 min.

The design for each series of experiments is explained in the corresponding paragraph of Results. Unless indicated otherwise the species of bird used as a stimulus was a Java sparrow (*Padda oryzivora*). The letter C- before training or learning indicates that a continuous procedure was used, and the letter D- indicates a discontinuous procedure. When D-training or learning is mentioned without qualification, animals received 30 trials a day with 10 min between trials.

RESULTS

1. *The effects of numbers of trials and duration of session on learning parameters*

Speed of learning. Sixty female mantids were randomly distributed in the following five groups of 12 animals each. (a) The 30-group-(10 m) received sessions of 30 trials a day, 10 min apart; (b) the 15-group-(10 m). sessions of 15 trials a day 10 min apart;

Table 1. Influence of number of trials per session and duration of session on the speed of learning

	e_2	e_3	e_4	e_5	e_6	e_7	e_8	e_9	e_{10}
30-group-(10 m)									
Mean	23.4	19.4	4.9						
S.D.	(±30.0)	(±28.9)	(±4.9)						
n of animals at *criterion*	7	8	12						
15-group-(10 m)									
Mean	74.4	49.6	37.1	30.5	18.2	13.4	9.2	4.7	
S.D.	(±23.5)	(±34.7)	(±30.7)	(±32.2)	(±17.5)	(±16.9)	(±10.5)	(±5.1)	
n of animals at *criterion*	0	2	2	3	6	8	9	12	
15-group-(23 m)									
Mean	70.4	56.4	36.8	35.5	24.6	23.5	8.2	3.4	2.7
S.D.	(±33.7)	(±32.4)	(±35.9)	(±34.6)	(±29.5)	(±18.2)	(±9.3)	(±5.6)	(±4.5)
n of animals at *criterion*	2	2	4	4	6	4	9	11	12
5-group-(10 m)									
Mean	98.8	98.4	94.2	89.6	85.0	85.8	78.8	69.2	60.8
S.D.	(±3.1)	(±4.5)	(±14.3)	(±18.9)	(±18.7)	(±20.5)	(±29.1)	(±31.7)	(±29.9)
n of animals at *criterion*	0	0	0	0	0	0	0	1	1
5-group-(85 m)									
Mean	97.9	95.8	94.7	95.6	91.4	84.3	73.9	66.8	69.7
S.D.	(±4.0)	(±6.7)	(±7.3)	(±5.9)	(±17.1)	(±20.0)	(±21.3)	(±31.7)	(±38.2)
n of animals at *criterion*	0	0	0	0	0	0	1	1	1

Table 2. Influence of number of trials per session and total time per session on retention

	Days after the second training session: 2		6	
30-group-(10 m)			e_r	
Mean			20.1	$\bar{D} = 6.2 \pm 13.3$
S.D.			($\pm$20.4)	NS
15-group-(10 m)			e_r	
Mean			87.9	$\bar{D} = 27.1 \pm 24.1$
S.D.			($\pm$16.2)	$0.005 > P > 0.001$
15-group-(10 m)	e_r			
Mean	45.2	$\bar{D} = 7.5 \pm 39.1$		
S.D.	($\pm$36.1)	NS		
15-group-(23 m)			e_r	
Mean			85.2	$\bar{D} = 23.5 \pm 35.1$
S.D.			($\pm$18.9)	$P \sim 0.025$
15-group-(23 m)	e_r			
Mean	48.8	$\bar{D} = 16.6 \pm 31.2$		
S.D.	($\pm$29.2)	NS		

(c) the 15-group-(23 m), sessions of 15 trials a day 23 min apart; (d) the 5-group-(10 m), sessions of 5 trials a day, 10 min apart; (e) the 5-group (85 m), sessions of 5 trials a day, 85 min apart.

In order to allow comparisons between groups, data from this series of experiments are presented as percentages of the maximum score obtained per animal per session during training. Animals were subjected to successive sessions either until all scores had declined to a value equal to or less than 15% (criterion), or until 10 days of training were given whichever was the score. Table 1 summarizes the results. All the mantis of the 30-group-(10 m) reached criterion in three sessions, those of the 15-group-(10m) in 9 sessions, and those of the 15-group-(23 m) in 10 sessions. In both 5-groups only one amimal reached criterion after 8–10 days of training. Comparison between mean precentages per session of different groups (unpaired t test, $\alpha = 0.05$) showed (i) that the level of responsiveness of the 30-group-(10 m) was significantly less ($P < 0.001$) than that reached by any other group during the same session, (ii) that the level of both 15-groups was less than that of both 5-groups for the same session ($P < 0.001$), and (iii) that no significant difference was found between groups with the same number of trials. Note that total training times for the 30-group-(10 m), the 15-group-(23 m) and the 5-group-(85 m) were similar, i.e. about 350 min from the beginning of the first trial to the end of the last trial. Thus, the rate of learning seems to depend on the total number of trials per session, and not on the total duration of the session nor the intervals between trials (provided the inter-trial interval is equal to or longer than 10 min).

Retention of learning. A further 60 female mantis were randomly distributed in five groups of 12 animals each, i.e. one 30-group-(10 m), two 15-group-(10 m) and two 15-group-(23 m). The training procedure was the same as that used for the corresponding groups above. All the groups were given three training sessions. The first two sessions were on consecutive days (e_1 and e_2). The 30-group-(10 m) received the third training session (i.e. the retention session, e_r) after a rest interval of 6 days. One 15-group-(10 m) and one 15-group-(23 m) received e_r after a rest interval of 6 days, and one 15-group-(10 m) and one 15-group-(23 m) after a rest interval of 2 days. Table 2 summarizes the results, $\bar{D}$ stands for the average of the differences between percentages of e_2 and e_r; P for the probability calculated using the paired t-test ($\alpha = 0.05$). After 6 days of rest interval, the 30-group-(10 m) showed good retention, i.e. $\bar{D}$ is not statistically significant. After 2 days of rest interval, the 15-group-(10 m) and the 15-group-(23 m) showed

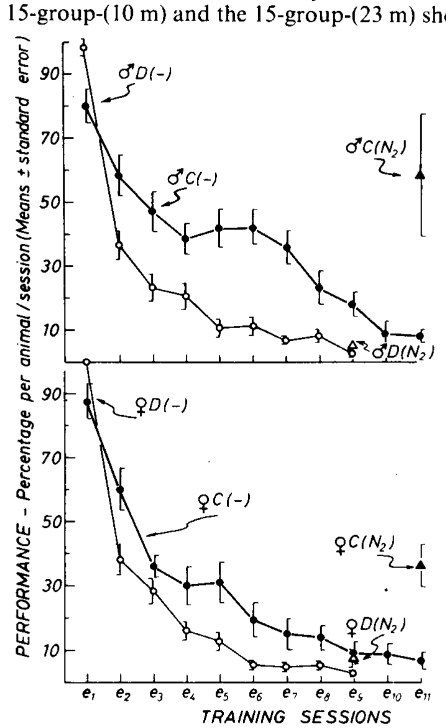

Fig. 1. Performance of different groups expressed as the mean percentage of the maximum response levels for each individual at the start of e_1. Upper graph: males. Lower graph: females. ——●—— continuous training (C), ---○--- discontinuous training (D). ▲: performance of C-groups after anoxia. △: performance of the D-groups after anoxia.

Table 3. Paired comparisons of data for the four groups without anoxia

Comparisons between sessions		Groups ♂ D (−)	♂ C (−)	♀ D (−)	♀ C (−)
e_1 vs e_3	D̄	75.1	41.0	72.4	51.3
	t	17.7‡	5.9‡	16.8‡	7.8‡
e_3 vs e_5	D̄	12.8	5.7	15.2	3.7
	t	3.8‡	0.8 NS	4.7‡	0.7 NS
e_5 vs e_7	D̄	4.1	6.9	8.0	15.0
	t	2.2*	1.2 NS	2.3*	3.4†
e_7 vs e_9	D̄	3.7	18.2	2.4	6.2
	t	2.7*	4.0‡	2.03*	2.4*
e_9 vs e_{11}	D̄	----	9.9	----	4.9
	t	----	3.0‡	----	2.3*

D̄ = mean of paired differences.
t = paired t test.
‡ stands for $P < 0.001$.
† stands for $0.01 > P > 0.001$.
* stands for $0.05 > P > 0.01$.
NS stands for no significant difference ($P > 0.05$).

a good retention also, i.e. neither D̄ is significant. Retention proved to be similar for the three groups, since differences between the corresponding D̄ are not significant (unpaired t test, $\alpha = 0.05$). On the other hand, after 6 days of rest interval, both the 15-group-(10 m) and the 15-group-(23 m) showed a sharp loss of retention, i.e. values of D̄ s are significant. This loss of retention was similar for the two groups, since the difference between their D̄s does not reach significance. Thus, the persistence of habituation depends only on the total number of trials per session, as is the case for the rate of learning.

2. Discontinuous and continuous training and the effect of anoxia; sex differences

148 male mantis were randomly distributed in two groups of 74 mantis each, i.e. D-group and C-group. D-group received nine training sessions ($e_1 \ldots e_9$) with the discontinuous procedure and C-group eleven training sessions ($e_1 \ldots e_{11}$) with the continuous procedure. Thirty-seven mantis of the D-group were subjected to anoxia immediately after the last trial of e_8, 37 mantids of the C-group were similarly treated immediately after the last trial of e_{10}. An equivalent distribution in groups was adopted for 148 female mantis. Thus, the final design comprised eight groups of 37 mantis each, i.e. ♂D (−), ♂ D (N_2), ♂ C (−), ♂ C (N_2), ♀ D (−), ♀ D (N_2), ♀ C (−), ♀ C (N_2), where (−) stands for training without anoxia and (N_2) for training with one period of anoxia.

Performances of the D-groups were recorded as scores of DRs, those of the C-groups as total time in minutes. In order to allow comparisons between these two groups, all results of this series of experiments are given as percentages of the maximum value obtained per animal during training. The effect of anoxia on the performance is assessed by comparing pairs of groups of the same sex subjected to the same type of training, but in which only one of the groups of the pair was subjected to anoxia. The following relationship was

Table 4. Analysis of variance on data per session of training groups: ♂ C (−), ♂ D (−), ♀ C (−), ♀ D (−)

		e_1	e_2	e_3	e_4	e_5	e_6	e_7	e_8	e_9
Training Procedure	F	10.80 $P<0.005$	15.99 $P<0.005$	9.73 $P<0.005$	10.41 $P<0.005$	7.92 $P<0.005$	29.29 $P<0.005$	29.54 $P<0.005$	11.84 $P<0.005$	17.69 $P<0.005$
Sex	F	0.14 NS	0.09 NS	0.40 NS	1.60 NS	0.21 NS	12.49 $P<0.005$	8.89 $P<0.005$	3.18 NS	2.13 NS
Interaction	F	0.003 NS	0.01 NS	2.16 NS	0.13 NS	0.45 NS	3.97 $P<0.05$	6.16 $0.025>P>0.01$	1.09 NS	2.52 NS

F = quotient of the estimated variance due to one factor over that due to individual differences.
NS = no significant difference ($P>0.05$).
Underlined figures stand for significant differences.

Table 5. Effect of anoxia on the performance of the following day (D- and C-training; female and male mantis)

Groups	e_n	$\bar{D}_e$ (e_1-e_{n+1})	$\bar{D}_c$ (e_1-e_{n+1})	% of loss of retention relative to control	
♀ D (N_2)	e_8	92.35	97.20	4.99	NS
♂ D (N_2)	e_8	92.86	95.95	3.22	NS
♀ C (N_2)	e_{10}	51.33	81.18	36.77	$0.01>P>0.005$
♂ C (N_2)	e_{10}	28.36	78.66	63.95	$0.01>P>0.005$

e_n = training session in which a N_2-shock was given.
e_{n+1} = training session that followed e_n.
$\bar{D}_e$ = average of the difference between values of e_1 and e_{n+1} of the groups that received an N_2-shock.
$\bar{D}_c$ = average of differences as $\bar{D}_c$ but corresponding to a similar group without N_2.
P = statistical probability (unpaired t test, $\alpha = 0.05$) corresponding to the difference between $\bar{D}_e$-$\bar{D}_c$.

used ($\bar{D}_c$-$\bar{D}_e$) × 100/$\bar{D}_c$, i.e. % loss of retention by experimentals relative to controls, where $\bar{D}_e$ stands for the average response decrement between e_1 and e_n in an experimental group, and $\bar{D}_c$ for the average between the same sessions in the corresponding control group.

Figure 1 presents performances of different groups expressed as means of percentages per animal per training session. Results for *all* the sessions are shown for the four groups that did not experience anoxia (white and black circles), i.e. ♂ D (−), ♂ C (−), ♀ D (−) and ♀ C (−). Results for groups ♂ D (N_2), ♂ C (N_2), ♀ D (N_2) and ♀ C (N_2), are indicated only for those sessions that were followed by anoxia (white and black triangles), since during the previous days their performances were similar to the corresponding control groups. A first inspection of Fig. 1 suggests that (a) animals trained with the C-procedure learn not to display DR, (b) speed of learning of D-groups seems to be greater than that of C-groups, (c) anoxia administered to the C-animals after 10 days of training has an amnesic effect, in spite of the fact that these mantids had learnt to virtually ignore the presentation of a bird, (d) learning curves of the C-male groups seem to be different in form from those of the C-female groups. Further analysis of these results is presented in Tables 3–5.

Table 3 presents paired comparisons of data for the four groups without anoxia. Results of e_1 are compared with those of e_3, e_3 with e_5, e_5 with e_7, e_7, with e_9 and e_9 with e_{11}. Differences are statistically significant for every comparison of both D-groups, i.e. ♂ D (−) and ♀ D (−) (paired-*t*-statistic, $\alpha = 0.05$). On the other hand, ♂ C (−) and ♀ C (−) show a sharp fall in the performance between e_1 and e_3, little change between e_3 and e_5, and a further marked decrement at the end of the training. However, the period of unchanged performance was longer for ♂ C (−) group than for ♀ C (−) group. This fact is better illustrated when values of e_3 vs e_7 are compared in both groups. For the ♂ C (−) group the mean of the paired differences per animal does not reach significance, but for the ♀ C (−) group the value of $\bar{D}$ is equal to 17.8, $t = 4.4$, $P < 0.001$. Similar results were obtained when the same analysis was performed on the four N_2-groups before anoxia.

Table 4 summarizes results obtained from an analysis of variance performed on data of groups ♂ C (−), ♂ D (−), ♀ C (−) and ♀ D (−). Factor 'training procedure' proves to be for all the sessions a source of variation that caused a mean square significantly greater than that derived from individual differences. However, in sessions e_6 and e_7, factor 'sex' shows significant differences between levels and a significant interaction with the factor 'training procedure'. Thus, this analysis indicates that no-DR learning takes place more slowly with the C procedure than with the D procedure and that the delay proved to be even greater for males than for females during e_6 and e_7. The same analysis of variance was performed on data from the other four groups but from e_1 to e_8, i.e. before anoxia, and similar results were obtained.

Table 5 illustrates the effects of anoxia on the performance of the following day in the four N_2-groups. Percentage losses of retention relative to controls are shown. *P* stands for the statistical probability (unpaired *t* test, $\alpha = 0.05$) corresponding to a difference between $\bar{D}_e$ and $\bar{D}_c$. This statistical analysis shows that after 8 days of D-training the N_2-shock has no amnesic effect either in female or male mantids. On the other hand, anoxia given after 10 days of C-training causes a sharp increase in the time during which the DR is displayed. This amnesic effect is seen in both sexes. An analysis of variance performed on data of the day following an N_2-shock for the four groups shows that only one factor, i.e. 'training procedure', caused a mean square significantly greater than that derived from individual differences ($F = 17.2$, $P < 0.001$). Factor 'sex' did not yield significant differences between levels of performance or significant interaction with the factor 'training procedure'.

In order to test if the waning response that was found with the C-procedure fulfills the parametric characteristics of habituation (Thompson and Spencer, 1966; Balderrama and Maldonado, 1971), the following experiments completed the present series.

Twenty-five male mantids received a training that was the same as the C (−) group up to session e_{10}. After e_{10}, training was withheld for 4 days, i.e. the rest period, and then a special session (ss) was given. It consisted of a training session lasting 4 hr. During the first 2 hr the original stimulus was presented, (*Padda oryzivora*), but during the last 2 hr a new stimulus was shown, i.e. a different species of birds, *Molothrus bonariensis*. This group gave results similar to the ♂ C (−) and ♀ C (N_2) groups up to e_{10}. After four days of rest period, response levels remained low during the first two hours of the special session (ss). In fact, the average of records corresponding to the first 2 hr of ss was not statistically different from that of e_{10} (paired *t*

Table 6. Scores during the first day of training (e_1): nitrogen shock given prior to training

Groups	(Mean ± S.D.) First 15 trials		Total of the 30 trials
Control	46 ± 17		69 ± 45
Anterograde control	47 ± 21		70 ± 30
1 day	50 ± 25		74 ± 50
2 days	44 ± 21		72 ± 45
4 days	43 ± 24		71 ± 48
8 days	46 ± 18		68 ± 55
	F	1.23	0.84
Analysis of variance	df1	5	5
	df2	234	234

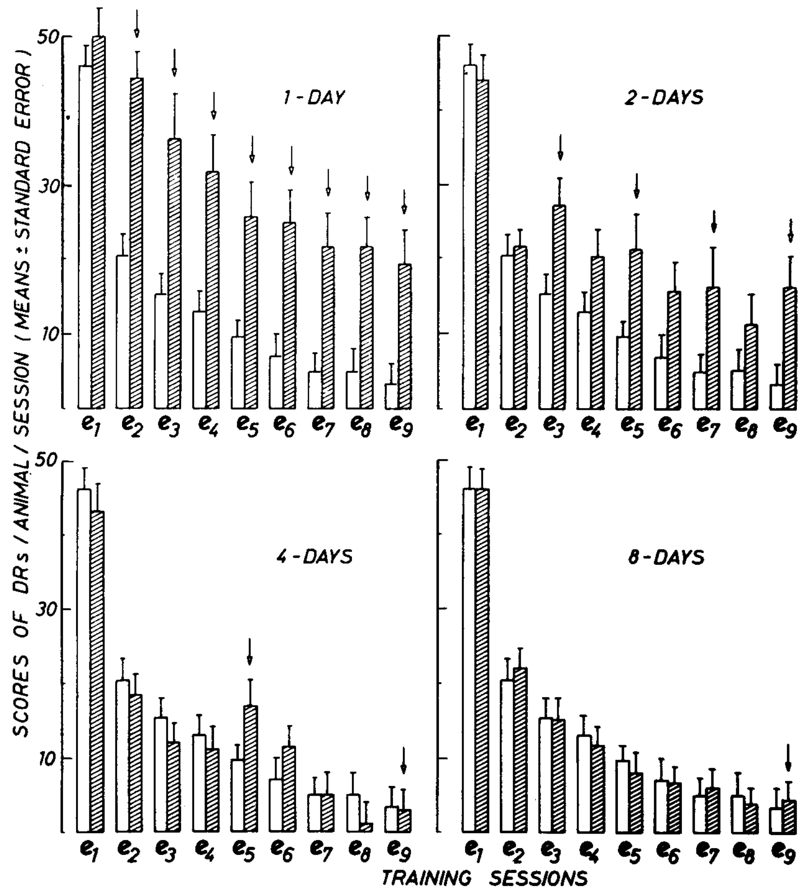

Fig. 2. Scores of DRs for the first 15 trials of every session. White bars: control group; striped bars: experimental groups, i.e. 1-day, 2-day, 4-day and 8-day groups. An arrow indicates that mantids received an N_2-shock immediately after the last trial of the previous session.

statistic, $\alpha = 0.05$). Thus, this group showed a very good retention after 4 days without training. However, when the new stimulus was suddenly presented after the first 2 hr of ss, DR immediately reappeared. Percentage values during the second 2 hr of ss went up to 65.6%, i.e. a mean that is statistically equivalent to that reached during e_1 (paired t statistic, $\alpha = 0.05$).

3. *The effect of anoxia at various times during training (D-procedure)*

240 Male mantids were randomly divided into six groups of 40 each and trained according to the D-procedure. The control group received nine daily training sessions which are denoted $e_1 \ldots e_9$. The anterograde control group received an N_2-shock 1 day before the only training session e_1. Experimental groups: 1-day group, nine daily training sessions, and one daily N_2-shock immediately after the last trial of each session; 2-day group, nine daily training sessions, and anoxia immediately after the last trial of e_2, e_4, e_6 and e_8; 4-day group nine training sessions, and anoxia immediately after the last trial of e_4 and e_8; 8-day group, nine training sessions, and anoxia immediately after the last trial of e_8.

In order to quantify loss of retention seen in a given session resulting from a N_2-shock received the day before, the percentage loss of retention is again used: $(D_c\text{-}D_e) \times 100/D_c$, where D_c stands here for the average response decrement between the first 15

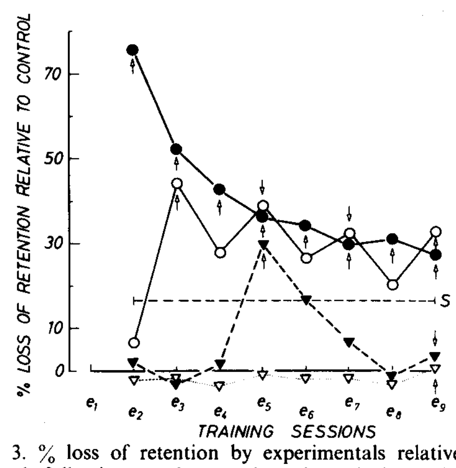

Fig. 3. % loss of retention by experimentals relative to controls following anoxia at various times during training. Arrows indicate retention values for the session on the day after anoxia. Zero denotes the control level and all losses greater than the level indicated by S were significant (t test $\alpha = 0.05$) ——●—— 1 day group, ——○—— 2 day group, – – –▲– – – 4 day group . . .△. . . 8 day group.

Table 7. Influence of lapse of time after training on the efficacy of anoxia

			Days after the second training session 1	6		
Control group	e_1	e_2		e_r	$\bar{D}_c$	
Mean	46.3	18.1		16.0	30.3	
S.D.	(±13.9)	(±19.3)		(±18.5)	(±12.6)	
		$\bar{D}=28.2$		$\bar{D}'=2.1$		
		(±13.5)		(±8.9)		
		$P<0.001$		NS		
N_2-e_2-group	e_1	e_2		e_r	$\bar{D}_e$	percentage loss of retention
Mean	46.0	18.2		38.2	7.2	
S.D.	(±14.9)	(±18.5)		(±19.4)	(±15.3)	76.2 ($0.005>P>0.001$)
		$\bar{D}=27.8$		$\bar{D}'=-20.6$		
		(±13.8)		(±22.9)		
		$P<0.001$		$0.01>P>0.005$		
N_2-5 days-group	e_1	e_2		e_r	$\bar{D}_e$	percentage loss of retention
Mean	52.3	26.7		42.6	9.7	
S.D.	(±8.9)	(±21.8)		(±13.9)	(±16.7)	68.0 ($0.01>P>0.005$)
		$\bar{D}=25.6$		$\bar{D}'=-15.9$		
		(±19.9)		(±20.1)		
		$P<0.001$		$P=0.005$		

$\bar{D}$ = average of differences between scores of e_1 and e_2.
$\bar{D}'$ = average of differences between scores of e_2 and e_r.
P = statistical probability (paired t test, $\alpha=0.05$) corresponding to $\bar{D}$ and $\bar{D}'$.
$\bar{D}_e$ = average of differences between values of e_1 and e_r corresponding to groups that received an N_2-shock.
$\bar{D}_c$ = average of differences as $\bar{D}_e$, but corresponding to the *Control group*.
P = statistical probability (no paired t test, $\alpha=0.05$) corresponding to the difference between $\bar{D}_e$-$\bar{D}_c$.
NS stands for $P>0.05$.
An arrow indicates the moment an N_2-shock was given.

trials of e_1 and e_n, respectively, for the control group, and $\bar{D}_e$ for the average of similar differences in a given experimental group.

Table 6 shows that scores during the first day of training, e_1, are similar for the six groups. In fact, analysis of variance on the scores for the first 15 trials or for all the 30 trials of e_1, indicates that differences among the six groups did not reach statistical significance. Thus, anoxia given 1 day before e_1, did not alter the DR scores during the first training session.

Figure 2 shows scores corresponding to the first 15 trials of every session. Experimental groups, i.e. 1-day, 2-day, 4-day and 8-day groups (diagonal striped bars) are compared with the performance of the control group (white bars). An arrow at the top of a bar indicates anoxia immediately after the last trial of the previous session. All the scores of the 1-day group proved to be greater than those of the control group for those sessions that were preceded by anoxia, i.e. e_2 . . . e_9 (t test, $P<0.05$ in all the comparisons). Scores of the 2-day group were similar to those of the control group for e_1 and e_2, but after the first N_2-shock the DR-scores increased. Two day and control group scores were significantly different after e_3. The 4-day group received two N_2-shocks, but only the first one elicited a clear increment in the scores. The 8-day group received only one N_2-shock after the eighth session, but no effect could be detected on the performance during e_9. Thus, these results suggest (a) that N_2 anoxia interferes with memory retention and (b), in addition, that the effect fades out with training. Figure 3 summarizes these results and indicates the level beyond which values become significantly different from controls. The 8-day group showed a degree of retention similar to that of the control group for all the training sessions, including e_9, i.e. anoxia at the end of e_8 did not impair retention. The 4-day group showed clear loss of retention in e_5 because of the first N_2-shock, and the effect is also apparent during e_6, but the second N_2-shock did not produce further impairment at e_9. The 2-day group gave a sharp fall in retention after the first N_2-shock and no subsequent recovery towards the control level. In the 1-day group (black circles), the first N_2-shock produced the greatest loss of retention and the subsequent preformance never reached the control level.

4. *The effect of lapse of time on memory retention through a period of anoxia*

Thirty-six male mantis were randomly distributed in three groups of 12 animals each, i.e. the Control group, the N_2-e_2-group and the N_2-5 days-group. All received first two consecutive sessions of 30 trials each, 10 min apart, i.e. e_1 and e_2, and after 6 days of rest interval a retention session, e_r. The Control group was not given any N_2-shock. The N_2-e-group was given an N_2-shock immediately after the last trial of e_2, and N_2-5 days-group an N_2-shock 5 days after the last trial of e_2.

Results are presented in Table 7, where means represent averages of scores corresponding to the first 15 trials of every session. An analysis of variance on values of e_1 for the three groups, indicated that differences among them do not reach statistical significance ($F=0.91$), likewise for an analysis of the mean differences between e_1 and e_2, $\bar{D}$ ($F=0.09$). The Control group showed a good retention after 6 days of rest interval, i.e. $\bar{D}'$ is not statistically significant. This result is consistent with the first series of experiments in which female instead of male mantis were used. On the other hand, an N_2-shock given immediately after e_2 or 5 days after e_2 produced a marked and similar impairment of retention, i.e. both values of $\bar{D}'$ are statistically significant and the difference between them does not reach significance (unpaired t test, $\alpha=0.05$).

The % loss of retention was calculated for each N_2-group (right side of Table 7). Both N_2-groups gave high percentages, 76.2 and 68.0%. Though these mean values are greater than the mean for animals that also received an N_2-shock immediately after e_2 but followed by only 1 day of rest interval (44.4%, 2-day group, Fig. 3) the difference is not statistically significant ($P>0.25$, unpaired t-test).

Thus, results suggest that the passage of time does not modify susceptibility to memory disruption by N_2-anoxia.

DISCUSSION

The experimental observations of this paper will be discussed in relation to the theory of the dual trace of memory, i.e. the dichotomy between short-term memory (STM) and long-term memory (LTM).

It has been argued that the STM–LTM classification oversimplifies an extremely complex situation (TULVING, 1970; GRIFFITH, 1970; ERVIN and ANDERS, 1970; WEISKRANTZ, 1970), and several hypotheses have been put forward concerning the different ways in which the two storage mechanisms might be related (e.g. MCGAUGH, 1969). Nonetheless, the theory is defined by certain constant concepts that can be roughly summarized in the following terms. (a) Memory consolidation is a time-dependent process; (b) STM accounts only for a brief retention, it is susceptible to agents that block neural activity of the CNS, and therefore, it is assumed to be based on orderly neural activities; (c) LTM, on the other hand, accounts for long retention, it is not sensitive to amnesic agents, and most probably it is founded on bases other than sustained neural activity, e.g. anatomical changes in a vast assemblage of synaptic pathways (ECCLES, 1969) or the synthesis of certain peptides (UNGAR and RUSSELL, 1972).

The results reported here do not seem to fit such a schematic set of assumptions. Consolidation of the no-DR memory appears to be event-dependent, instead of time-dependent. Mantids that receive two sessions of D-training prove to have a long retention (6 days, at least), i.e. like LTM, but this long memory is dramatically disrupted by anoxia with nitrogen, i.e. like STM. Thus, it is suggested that this learning process entails a long-lasting and simultaneous activity of two different mechanisms, i.e. one accounting for a trace sensitive impairment (S memory) and the other for an insensitive one (I memory). The relative participation of these two traces seems to change in a manner contingent on the degree of training rather than lapse of time, the S process declining in importance relative to the I process. After a certain number of successive sessions, (5–8), the system would reach a steady-state and memory would be wholly in the I form.

ERBER (1975a,b,) and MENZEL *et al.*, (1975) have studied this subject analyzing a learning process in another insect, i.e. the time course of a correct choice in the honey bee, also using N_2 anoxia as an amnesic agent, and in addition ECS, CO_2-narcosis and cooling. Their results are not directly comparable with those of the present paper, since two very different experimental situations are involved: the learning process of the mantis is a slow process whereas that of the honey bee is a case of one trial learning. However, similar conclusions are reached as regards the possibility of a double mechanism acting in parallel. In fact, ERBER (1975a,b) proposes that the time course of the choice reaction in the bee can be described by two processes of memory formation, which have different physiological bases but which work closely together.

The S memory in no-DR learning could be based on orderly neural activities, i.e. like the STM, and the I memory on a 'molecular' trace, i.e. like the LTM. JAFFÉ and MALDONADO (1979) have found in the mantis a chemical correlate to the process of learning not to attack a mobile star and preliminary work in our laboratory suggests similarly that certain amine-containing components appear during no-DR learning. If this preliminary result is confirmed, the above proposal could be tested. It would be expected that the chemical correlate became more evident during the training process, reaching a maximum when the I memory became fully dominant, (after 5–8 days of D-training).

With the continuous training schedule, 10 sessions are necessary for the response level to fall as low as that reached after 8 days with discontinuous training. However, in spite of this similarity, memory appears to be consolidated during discontinuous training but not during continuous training. This contrast could be accounted for by the different shapes of the learning curves in the two cases (Fig. 1). Mantids trained with the D-procedure show responses around 10% maximum during four successive days, e_5–e_8, whereas those trained with the C-procedure show comparably low means only during 1 day, e_{10}, with males, or during 2 days, e_9 and e_{10}, with females. Thus, it is possible that for complete transfer to the I 'register' to take place, not only must the level of response decline to a minimum, but it must also remain there during a certain number of sessions. Obviously, it is important for the validity of the central hypothesis of the present paper that this possibility be investigated further.

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