Intertrial interval and passive avoidance learning in *Octopus vulgaris**

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When *Octopus vulgaris* were trained on a passive avoidance task at various intertrial intervals from 0.05 to 10 min, acquisition rate was maximal at the intermediate intervals, a finding similar to those obtained with rats. Explanations involving fear are thought to be inadequate and the phenomenon is interpreted in terms of short-term memory.

Biphasic curves of retention performance after one-trial passive avoidance training have been found with both mice (Zerbolio, 1969; Robustelli, Geller, & Jarvik, 1970) and fish (Riege & Cherkin, 1972). A particular feature of these findings is a low level of performance immediately after the training trial. With octopuses trained to a criterion over a short series of trials on a passive avoidance task, we have obtained multiphasic retention performance curves that start high (Sanders & Barlow, 1971, and in preparation).¹ In these experiments, however, any initial rise in the level of performance would presumably occur during training and, thus, be obscured. We decided to investigate the problem by studying the rate of learning at different intertrial intervals. If, after a single trial, retention performance is initially low, subsequently increases, and then decreases, the acquisition rate over a series of trials should be an inverted U-shaped function of intertrial interval (ITI).

METHOD

Octopus vulgaris of 200-400 g and both sexes were individually housed in cream-colored plastic tanks measuring 100 x 28 cm with a seawater depth of 38 cm. During an initial adaptation and pretraining period, the octopuses were fed crabs and the latency of attack was recorded. Only octopuses that were attacking crabs readily (three attacks completed within 15 sec on 3 successive days) were used for training. The passive avoidance training began on the following day. At the start of each trial, a crab tied to a transparent plastic rod was placed on the floor of the tank about 50 cm from the octopus. When the octopus attacked, the crab was removed and the octopus given a 10-V shock on the arms by means of two electrodes mounted on a probe. An attack was recorded whenever it became necessary to remove the crab in order to prevent the octopus's touching the crab with its arms. Training was continued to a criterion of no attack for 1 min, during which the majority of octopuses made no movement toward the crab. Thus, each trial terminated with an attack reinforced by a shock, except for the criterion trial, which terminated after 60 sec with no attack on the crab. Octopuses that reached criterion in two trials or less were discarded. The nine animals thus excluded from a total of 114 came from all the groups except the 10-min group.

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RESULTS

In Experiment I a U-shaped relationship was found between trials to criterion and ITI (Table 1). Analysis of variance indicated that a significant difference existed between the groups ($F = 4.81$, $df = 4/40$, $p < 1\%$). Both the 1- and 2-min ITI groups required fewer trials to reach criterion than the 0.05-min ITI group (both $ps < 1\%$) or the 10-min ITI group (both $ps < 5\%$).

The results of Experiment II, which included a group trained with an ITI of 30 sec, confirmed those of Experiment I. Analysis of variance indicated a significant difference between the groups ($F = 3.70$, $df = 5/54$, $p < 1\%$). The 1-min ITI group reached criterion in fewer trials than the 0.05-min ITI group ($t = 2.94$, $df = 19$, $p < 1\%$), the 0.5-min ITI group ($t = 2.91$, $df = 18$, $p < 1\%$), and the 10-min ITI group ($t = 2.11$, $df = 17$, $p < 5\%$). The 2-min ITI group required fewer trials to reach criterion than the 0.05-min ITI group ($t = 2.46$, $df = 18$, $p < 5\%$) and the 0.5-min ITI group ($t = 2.21$, $df = 17$, $p < 5\%$) but was not significantly different from the 5- or 10-min ITI groups in this respect.

In both experiments (Table 1), the mean number of trials to criterion was clearly a significant U-shaped function of ITI. Details of the changes in the median latency of attack over Trials 4-9 are presented in Fig. 1, in which the data from Experiments I and II are combined. The major change in attack latency occurs very rapidly over the course of one to two trials. It is apparent that on Trial 6, when the majority of octopuses in the 0.05-, 0.5-, 5-, and 10-min ITI groups are still

Table 1
Mean Number of Trials Required to Reach Criterion With Training at Various Intertrial Intervals (ITI)

ITI (Min)	Experiment I			Experiment II		
	N	Mean	SEM	N	Mean	SEM
0.05	9	8.7	0.83	11	9.5	1.19
0.5				10	8.6	0.83
1	9	5.7	0.41	10	5.5	0.67
2	9	5.4	0.47	9	6.3	0.62
5	9	7.4	0.67	11	6.3	0.62
10	9	7.7	0.67	9	7.6	0.71

Fig. 1. Median latency of attack in seconds for each ITI group on Trials 4-9. On reaching criterion, individuals are included as > 60 sec. The data from Experiments I and II have been combined.

attacking the crab with latencies of less than 15 sec, the majority of the 1-min ITI group have surpassed the 60-sec criterion.

DISCUSSION

Improvement in the rate of acquisition as ITI increases is a well established phenomenon (Murphy & Miller, 1956; Thompson & Pennington, 1957; Levine & England, 1960; Brush, 1962; Brush, Myer, & Palmer, 1964; Pinckney, 1966, 1967; Sansone & Bovet, 1970). Two of these reports describe a subsequent decrease in acquisition rate at longer ITIs. Thompson and Pennington (1957) trained rats on a shock-motivated visual discrimination task and found that errors to criterion were a U-shaped function of ITI, with optimum learning at a 3-min ITI. Using an active avoidance task, Brush (1962) obtained a similar result, with optimum performance at an ITI of 5 min. The present experiments provide a striking parallel to these results and extend the generality of the finding from rats to octopuses (Phylum Mollusca).

The U-shaped curve was explained by Brush (1962) in terms of the reduction in conditioned fear as ITI lengthens. According to this hypothesis, the faster acquisition rate found at intermediate ITIs occurs as a

result of the greater reinforcement provided by the fear reduction. The subsequent decrease in acquisition rate at even longer ITIs is attributed to insufficient motivation resulting from too great a reduction of the fear conditioned to the apparatus cues. While this hypothesis adequately explains the results obtained with active avoidance tasks, it is not compatible with the present finding that similar effects can be obtained with passive avoidance training. An improvement in the performance of a passive avoidance task should be accompanied by an increase rather than by a decrease in the level of conditioned fear.

The U-shaped curve obtained with passive avoidance training might be accounted for by a gradual increase in generalized fear followed by a decline at longer intervals. Although this point has yet to be tested directly, two sources of evidence suggest that this is not the best explanation. First, direct study of the incubation of fear in rats and mice indicates that it increases over a period of at least several hours (Allen & Mitcham, 1970; Robustelli et al, 1970). Second, the type of passive avoidance training used with the octopuses in the present experiments is thought to produce specific learning not to attack the crab rather than a general reduction in the level of attack (Sanders & Barlow).¹

An alternative explanation is that the behavioral expression of the memory record is not maximal immediately after an event but requires a short time to reach a peak. The experiments of Zerbolio (1969), Robustelli et al (1970), and Riege and Cherkin (1972) support the view that, at least under some conditions, there is a measurable rise as well as a fall in short-term memory (STM). The improved acquisition rate observed as ITI increases could result from the cumulative effect of an initial rise of STM. Optimum conditions would be reached when the length of the ITI coincided with the peak of STM, while the eventual decrease in acquisition rate would correspond to the subsequent decline of STM. This interpretation of the U-shaped function between acquisition rate and ITI has the advantage of being equally applicable to both active and passive avoidance tasks.

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NOTE

1. Sanders, G. D., & Barlow, J. J. Retention performance after shock avoidance training in *Octopus vulgaris*. In preparation.

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