

## LEARNING IN THE CUTTLEFISH, *SEPIA*

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**Abstract.** The visual attack of the cuttlefish, *Sepia* (Mollusca: Cephalopoda) was used as a system to examine factors involved in learning. Cuttlefish shown prawns behind glass soon learn to stop striking at them, and the level of striking and its rate of waning were compared during continuous and repeated presentation (at different intervals). It was found that the level of striking was inversely related to the level of negative reinforcement and that the later phases of the attack wane faster than the earlier ones. Learning to suppress one stage of the attack may be contingent upon having learned to suppress the subsequent stage. If the striking response is allowed to recover after it has waned it is found that recovery takes place in two stages and it is suggested that this reflects the operation of separate short-term and long-term memory systems with parallel entry.

Students of learning at the behavioural level require a relatively simple response for investigation. The response should be easy to elicit, it should be discrete and clear cut and, if possible, it should be quantifiable. Since the ultimate aim must be to relate behavioural findings to the organization of the brain, it is appropriate to choose an animal whose central nervous system is reasonably well understood. For these reasons we have turned our attention to the feeding response of a cephalopod, the common cuttlefish, *Sepia officinalis*, and examined how this response alters when prey are presented behind glass.

*Sepia* is an active carnivore, feeding on fish, prawns, crabs, and other crustaceans. It may catch slow-moving prey with its eight short arms, but swifter animals are caught with the suckers on the terminal clubs of the long paired tentacles (Boycott 1958). These are shot out very rapidly at the prey, after the cuttlefish has gone through a clearly defined and relatively slow series of preparatory motor acts (Messenger 1968). Unlike the *Octopus* attack on crabs (Maldonado 1964), which is a fluid sequence of motor activity ending with a large, entire animal spread-eagled over its prey, the *Sepia* attack shows a number of separate components culminating in a precisely directed, all-or-none strike by the tentacles at a prawn that is considerably smaller than the cuttlefish.

It has long been known that cuttlefish can learn not to strike at prey animals behind glass; Sanders & Young (1940) showed that they can discriminate between a prawn and a 'prawn-plus-white-circle' on this basis. This was incidentally, the first demonstration that the cuttlefish attack is a purely visual response

(Messenger 1968), a fact that is exploited in this entire series of experiments.

Later Wells (1958, 1962) used a similar technique to investigate the behaviour of newly-hatched *Sepia*. He placed prey animals in a glass tube and was able to show that while adults quickly learned not to eject their tentacles under these circumstances, the young animals did not. These results were of great interest in themselves but they did not extend to a consideration of the detailed nature of the learning curve in the adult or of factors influencing it. The present series of experiments considers these points in detail, especially the way learning affects the sequence of motor acts that constitutes the attack. Evidence is also presented that we are dealing here with 'associative learning' (Thorpe 1963) and we finally examine evidence that this learning involves separate short-term and long-term memory systems (STM, LTM) with parallel entry. Where possible we relate the results to the organization of the cuttlefish brain as this is known from the detailed study of Boycott (1961).

### Methods

Subjects were adult cuttlefish, *Sepia officinalis* L. (Mollusca: Cephalopoda), captured in the Bay of Naples and kept separately in grey plastic tanks (100 × 30 × 50 cm) containing running sea-water to a depth of 40 cm. The animals, of between 80- and 170-mm dorsal mantle length, were mostly males that had been netted in clear water after approaching a lure female tied to a line. They were therefore in excellent physical condition and nearly all of them survived for more than a fortnight after these experiments had finished. Data were collected at Naples in January 1969 and the Spring of

1969, 1970, 1971, and 1972 (water temperatures were between 15° and 20°C); unless significant differences in mean attack-level were found between groups, data from different times were often pooled. It is emphasized that all the animals in all the experiments were naïve at the outset; that is, each animal was used once only in any of these experiments and then discarded (to another series of experiments on the control of the attack).

### Selection

Experiments were carried out only on animals that were attacking prawns. On the day after the cuttlefish had arrived in the aquarium, it was shown a prawn tied to a thread. If the prawn was attacked it was removed before it could be seized; if not, it was removed after 20 s and the cuttlefish was tested again the next day, and so on. Attacking animals were used in experiment on the same day, though necessarily at different times. There was no correlation between performances and time of testing. Experiments were generally performed between 09.00 and 21.00 hours, always under electric light (40-W fluorescent strips, 1 m above the water surface). Most animals attacked (and were, therefore, tested) on the third to fourth day after capture.

### The Experiment

The basic experiment was very simple. A transparent tube filled with sea-water and containing two prawns was placed in the tank with a cuttlefish, and the amount of time it spent attacking (and the number of strikes it made in a given time) was recorded.

The tube was of clear Perspex (to avoid writing 'transparent plastic' every time, the shorthand: 'glass' is used throughout the text) 77 mm in diameter (3-mm wall) and 520 mm high, mounted on a square base of the same material. The prawns were *Leander* sp. about 55 mm long (rostrum-telson) and two were used to increase the chance of having a moving prawn in the tube, movement being extremely important in eliciting an attack from a cuttlefish. Even so, pilot experiments showed that two prawns can remain still for long periods, and to overcome this a thin transparent Perspex rod (1 m long) was placed inside the tube and 'jiggled' once every minute, on the minute, to ensure that the prawns moved at least some of the time. This is an undoubted fault in the experimental design but, we think, not a serious

one (see Discussion). The tube, which was kept scrupulously clean, was very gently introduced by hand into the tank and set down about 60 cm away from the cuttlefish, which was generally at the back of the tank in the shadow of a lid; the observer remained motionless in front of the tank.

The tube was either left in continuously or removed and replaced at regular intervals; the lengths of presentation (or of interval) were varied; and other factors in the experiment were also manipulated. Details of these variations are described with each experiment. Where possible large numbers of animals were used; no group contains less than eight animals. Animals were allotted to treatments randomly (playing cards).

## Results

### I. The Waning of a Response

The attack by a cuttlefish on a prawn comprises three stages, and it is first necessary to restate the main features of each stage (Messenger 1968) as they occur in this modified, experimental situation. Then follows an analysis of the waning of the different stages of the response, and especially the waning of striking as a result of continuous and repeated stimulus presentation. It was felt worthwhile to make such a comparison as it is by no means certain that the waning occurring in these two situations is the same (Hinde 1970).

(1) **The response.** When a tube of prawns is placed in the tank the cuttlefish, at the far end of the tank, fixates the prawn first monocularly and then binocularly, after turning its head and body so that the prawn lies straight ahead of it, about 60 cm away (Fig. 1A). This first stage, which is termed attention, is also characterized by strong colour changes and erection and waving of one or two pairs of arms.

In the second stage, positioning, the cuttlefish swims down the tank towards the tube, and pauses a few centimetres away from it for several seconds, while showing waves of colour changes over the entire body (Fig. 1B). The exact distance at which it rests is a function of its length (with animals of the size used here it was about 5 cm); and experiment has shown that unless the cuttlefish can reach this attacking distance it will not eject its tentacles (Messenger 1968), a feature made use of in a later experiment. Both these first stages are relatively slow and are regulated by visual-feedback; if the prawn moves, for example up the tube, the cuttlefish

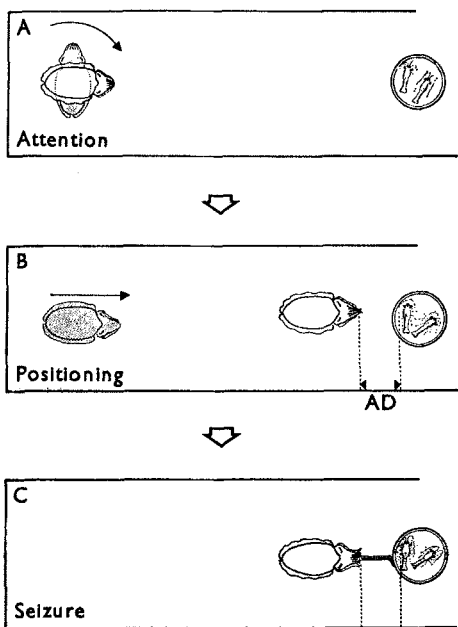


Fig. 1. The three stages of the attack and the experimental situation. AD is the attacking distance.

adjusts its position to maintain the attacking distance (Messenger 1968).

The third stage, seizure, is extremely rapid and under open-loop control (Messenger 1968). Both tentacles are ejected from between the parted arms to reach the prey (here, the glass) in about 15 ms (Fig. 1C). The tentacles hit the glass, apparently with some force; sometimes the strike glances off the tube but generally the suckers at the tentacle tips adhere to the surface of the glass and the tentacle shafts are thrown into folds. As the tentacles are withdrawn the shafts straighten, the suckers are pulled off the glass and both tentacles retract completely into the pockets below the eyes. Not until this is done can they be ejected again. The act of seizure, is, therefore, all-or-none, and this act, which we term a strike (cf. the 'stab' of Wells 1958, 1962) is the culmination of the attack sequence. The number of strikes per unit time is a most useful measure of the strength of the response at a given period.

In the laboratory, with free prawns, about 90 per cent of strikes are successful first time (Messenger 1968) and the prawn is brought back to the arms to be manipulated into the mouth. In this particular experimental situation, as might be expected in a cephalopod, the animal does not go on attacking the inaccessible

prawns for long: the rate of striking soon begins to diminish in a way that will now be examined.

(2) **The waning of the different stages of the response** ( $N = 30$ ). After a few trial observations, thirty naïve animals were observed throughout a continuous exposure of 20 min to prawns in a tube. During the presentation the responses were recorded in 10-s units. If an animal showed attention or positioning in any unit, even for 1 s, this unit was recorded as 'positive' for either attention or positioning. To measure seizure the actual number of strikes per unit was recorded. This gave a reasonably precise resolution of the way in which striking waned, but a very crude measure of the course of the earlier stages of the response.

To see how each component of the attack sequence wanes, we can compare for a given interval the time spent in attention, the time spent in position and the number of strikes. To compare these values it is convenient to relate them to the initial level of the response and express them as percentages of this (Fig. 2). In this figure the results have been plotted for periods of 5 min; for instance, the number of strikes in the second period was about a quarter that in the first.

From the figure it is clear that using this measure attention wanes very slowly indeed, that positioning wanes more rapidly, and that striking wanes most rapidly of all (this is also true if the results are plotted in absolute terms). During the last 5 min the animals were showing attention at the 75 per cent level, but positioning was less than 50 per cent, and the number of strikes was less than 20 per cent the initial level. This, of course, reflects what is seen when an individual animal is observed. The cuttlefish may soon give up striking but it will stay close to the tube at first, perhaps moving round it at the attacking distance and changing colour strongly; after a while it will back off for a short time and then return, perhaps making a strike, then retreat again all the while fixating the prawn. Only towards the end of the 20-min period might it turn away, so that the prey would no longer be seen binocularly.

Because attention and positioning wane so slowly and because it is difficult to quantify more precisely the behaviour during the first two stages, it seemed profitable to consider henceforth only the waning of the third stage, striking.

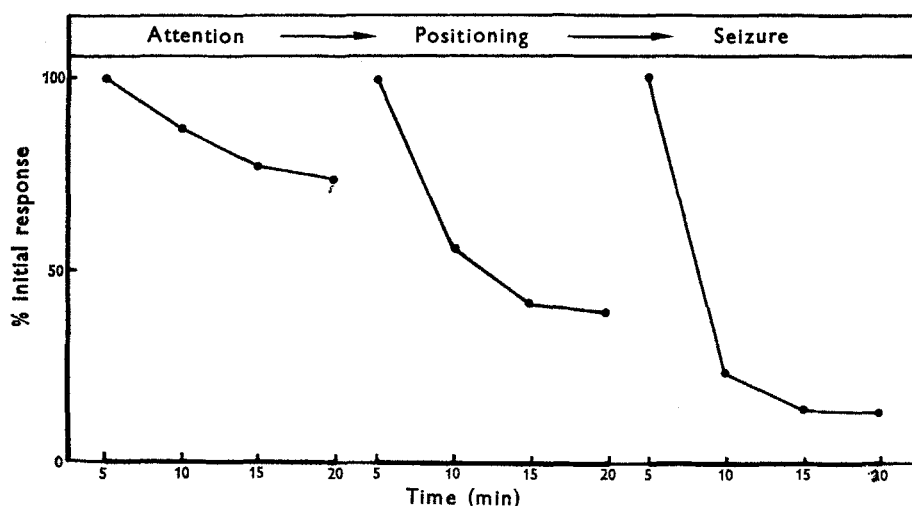


Fig. 2. The waning of the three stages of the attack during 20-min continuous presentation. Data is plotted in 5-min blocks and related to the level during the first 5 min ( $N = 30$ ).

### (3) The waning of striking during continuous presentation.

(a) *Twenty minutes* ( $N = 30$ ). So far, for purposes of comparison, we have only been considering waning relative to the initial level of the response. The way the absolute level of striking declines with time is shown for the same group of animals in Fig. 3a. Overall, the group made 441 strikes (mean = 14.7) during a 20-min presentation, but clearly most of these were made during the first 5 min when the mean level of striking was about ten. There was a considerable drop in strike level from the first to the second period; but by the third 5-min period the strike level is apparently approaching a steady value.

(b) *Five minutes* ( $N = 245$ ). In fact two-thirds (66.4 per cent) of all strikes were made in the first 5 min. (Indeed over half of all the strikes were made in the first 3 min.) Because of this the behaviour of a much larger number of animals participating in another experiment was subsequently observed and recorded for the first 5 min only. Data from these animals were pooled with those from the first group, and this enables us to look more closely at the waning over the first 5-min period in a relatively large group of animals ( $N = 245$ ) (Fig. 3b). Two points deserve mention: the waning process is reasonably linear at this stage and the steady level is not reached in the first 5 min. This agrees

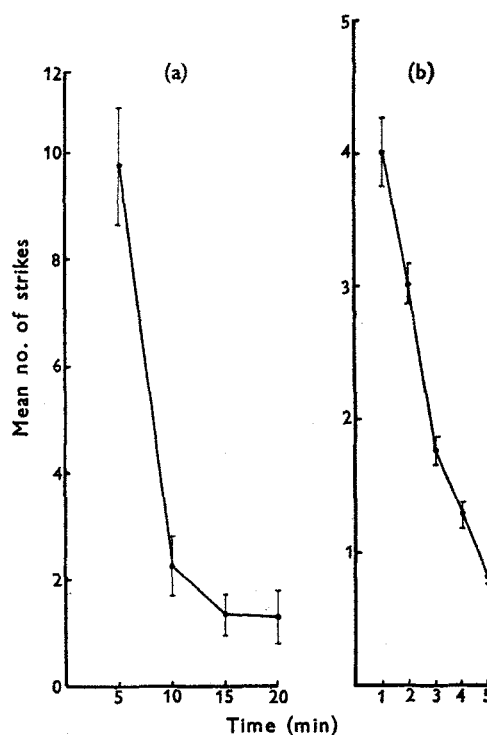


Fig. 3. Waning of seizure in absolute terms, (a) over 20 min (plotted in 5-min blocks) ( $N = 30$ ) and (b) over 5 min (plotted in 1-min blocks) ( $N = 245$ ). Bars indicate SE of mean.

with data in Fig. 3a. Overall, the group made 2674 strikes in the 5-min period (mean = 10.91) and about two-thirds of these (1731) were made in the first 2 min of presentation. Waning of this response is clearly a very rapid process indeed (cf. Hinde's chaffinches, 1954).

The behaviour during the first 5 min can be further analysed into units of 10 s. Such analysis (the finest resolution available) makes the interesting point that the maximum rate of striking is not reached until the second period of 10 s when the mean number of strikes is significantly higher than in the first ( $t = 3.35$ ,  $df = \infty$ ,  $P < 0.001$ ). This, which is shown in Fig. 4, cannot be entirely explained away as being due to the time necessary to approach:

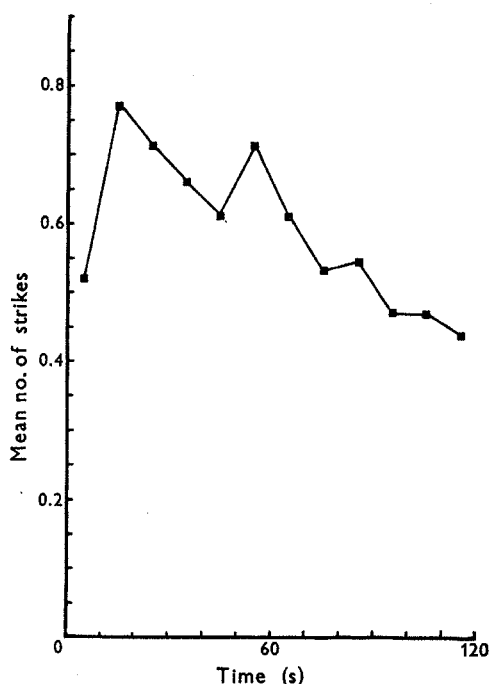


Fig. 4. Waning of seizure during the first 2 min of presentation, broken down into 10-s blocks ( $N = 245$ ).

it seems that there is some kind of 'warm-up' period (see Discussion). It is also noteworthy that the curve is irregular. Although this may just be 'noisy' data it is emphasized that the curve is the mean of no less than 245 individual animals. These irregularities may reflect the complexity of the process(es) underlying waning and must not be automatically dismissed.

Finally, if we record the latency to the first strike and plot it as a frequency diagram, it is

at once clear (Fig. 5) that most animals attack in the first 10 s, even though the maximum striking rate is not reached until the second 10-s period.

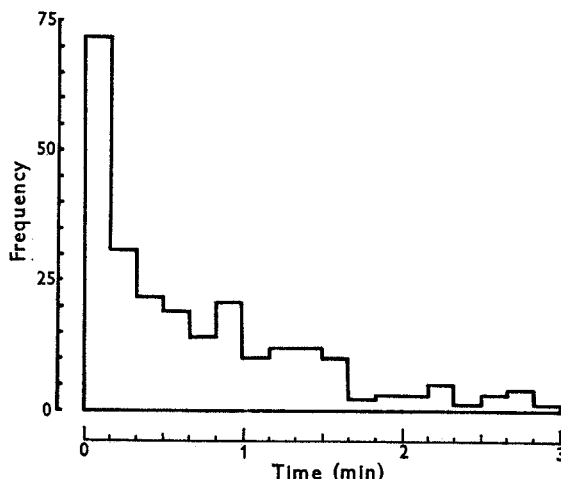


Fig. 5. Latency to first strike, plotted in 10-s intervals ( $N = 245$ ).

The criterion for acceptance was an attack within 3 min. Animals that did not attack the prawns in that time were discarded; they were few.

**(4) The waning of striking during repeated presentation** ( $N = 40$ ;  $N = 30$ ). Forty naïve animals were shown prawns in a tube for eight successive trials of 3 min each. As can be seen in Fig. 6 the absolute number of strikes falls off dramatically: for example, the number on the third trial is less than half that on the first, while the number on the fourth is less than a quarter that on the first.

For comparison, the behaviour of a group of animals ( $N = 30$ ) during continuous presentation is also indicated in Fig. 6. These are animals that had been shown the prawns continuously for 20 min (Section I, 3): here the data has been re-analysed and plotted in six, 3-min blocks, plus a 2-min one. It is at once apparent that the response wanes at a similar rate in both situations, at least when waning is measured in absolute terms. Consider, for example, the fall in strikes from first to second trial or the way that asymptote begins to be approached at about the fifth to sixth trial or after 15- to 18-min exposure. Unfortunately, there are three objections to making a strict comparison. First is an important methodological point. During repeated stimulus presentation the tube was

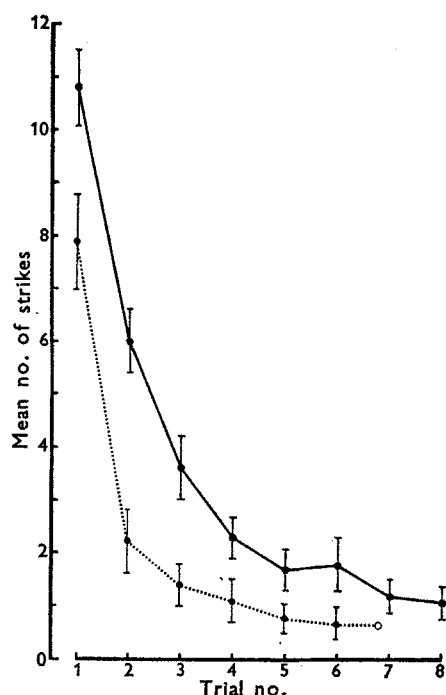


Fig. 6. The overall waning of seizure during repeated presentation (unbroken line;  $N = 40$ ), compared with that during continuous presentation (dotted line;  $N = 30$ ). Waning is expressed in terms of absolute strike level. Bars indicate *se* of mean.

continually being removed and replaced: such disturbance was not controlled for in the group tested continuously. Second, the 'continuous' group was not tested at the same time as the 'repeated' group and, third, the level of attack by the 'continuous' group on initial presentation was significantly lower ( $t = 2.56$ ,  $df = 68$ ,  $P < 0.02$ ). This group was tested in January (1969) instead of May and the difference in strike-level may be a consequence of a temperature difference of about  $5^{\circ}\text{C}$ .

With such a caveat we can only say that the course of waning, as measured in absolute terms, appears to be very similar during both continuous and repeated stimulus-presentation. It is worth making the point, in Fig. 7, that in relative terms the response appears to wane faster when presentation is continuous, at least in the early stages (see Discussion).

(5) **The effect of interval length on rate of waning** ( $N = 40$ ). With a series of repeated presentations one might expect that the response would wane more slowly if a long rather than a short interval separated trials. To test this,

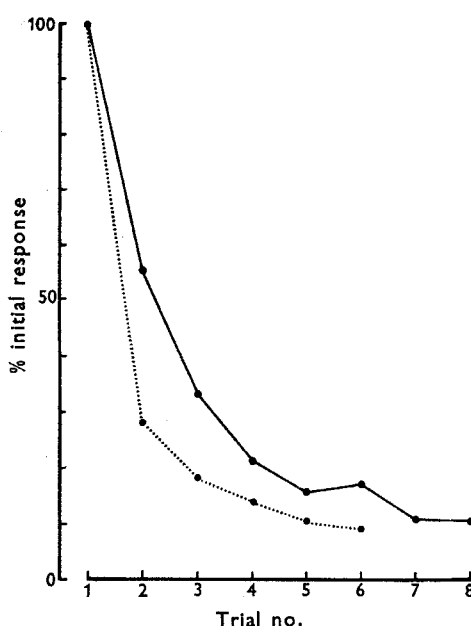


Fig. 7. The waning of seizure relative to the initial strike level (conventions as in Fig. 6).

forty animals were divided randomly among four treatments, each animal receiving its eight trials at the same interval, which was either 15 min, 30 min, 1 hr or 2 hr. The results are shown in Fig. 8, and at first sight it does appear that waning is faster at higher frequencies of presentation. This is not borne out by analysis of variance, however, using the non-parametric method: Kruskal-Wallis one-way (Siegel 1956) because the unequal variances invalidate use of the  $F$ -test. Even on the third trial, where the spread of strike level is greatest, the variation between treatments was no greater than that among them ( $H = 4.49$ ,  $df = 39$ , NS). On present evidence, then, we must conclude that, for repeated presentations of 3-min duration, the rate of waning of the response is independent of the length of interval between presentations. Obviously this does not preclude the possibility that interval length could have an effect with a different length of presentation and evidence is presented later that suggests that it does.

Although data from the animals tested at intervals of 15 min seem especially 'noisy' this may be a genuine effect. On the whole the data from the forty animals is not excessively variable, especially by cephalopod standards. Thus, although animals were randomly allotted to different groups prior to the first trial, there was

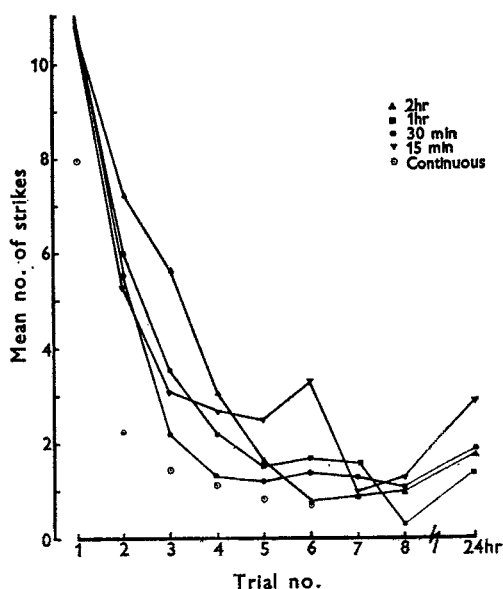


Fig. 8. The effect of interval-length on waning, measured in absolute terms. The eight trials, lasting 3 min each, were separated by either 15 min, 30 min, 1 hr or 2 hr ( $N = 10$  each treatment); cf. continuous presentation ( $N = 30$ ).

very close agreement indeed between performance on that trial (mean number of strikes 10.8, 11.0, 10.9 and 10.6 for each group). Because data for animals tested at intervals of 30 min give a very regular curve this interval was used in all subsequent experiments involving repeated presentation.

(6) **The behaviour during each trial** ( $N = 40$ ). This last experiment is in effect a series of separate continuous presentations. How does the response wane within each of these presentations? Do the rates of waning alter with time?

The answers to these questions are shown in Figs 9 and 10. In Fig. 9 we plot the absolute level of strikes (in  $\frac{1}{2}$ -min units) during each of the eight trials, for all four interval groups. It can be seen at once that despite the overall waning shown by each group the response does not decay smoothly. The data for the animals tested at intervals of 30 min again give the smoothest curve, but even here there are pronounced irregularities during the sixth and seventh sessions. With the other treatments the behaviour during both earlier and later trials is even more erratic. It is difficult to dismiss

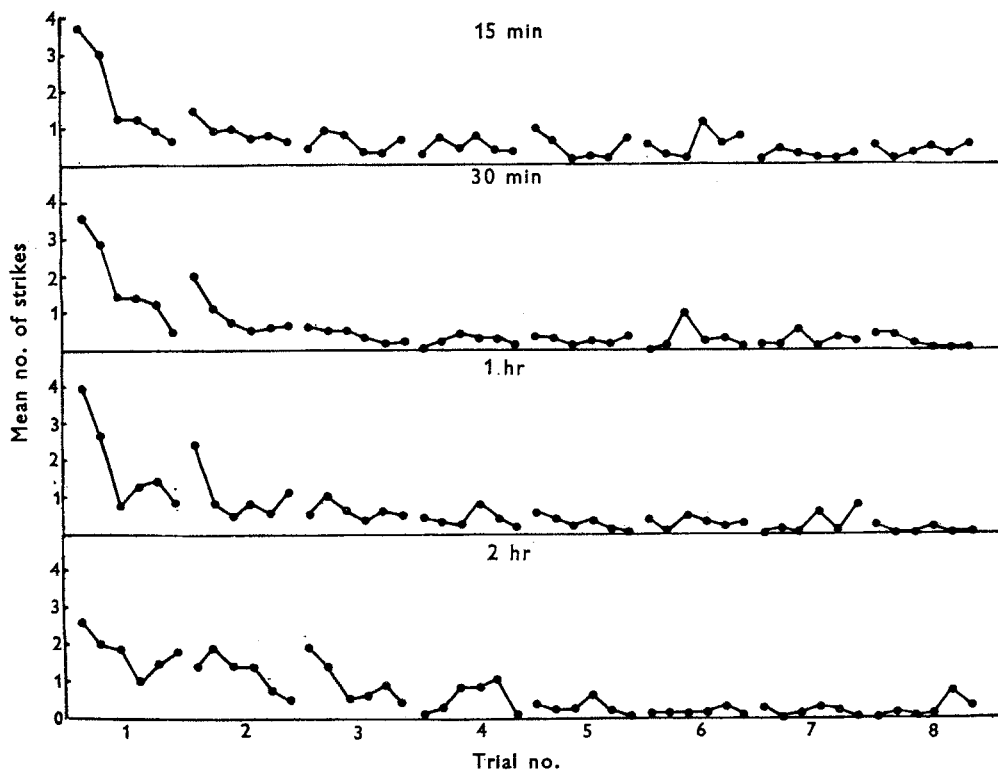


Fig. 9. The course of waning during individual trials presented at four different intervals (for each  $N = 10$ ); the absolute level of strikes per  $\frac{1}{2}$ -min unit is shown for each trial. Note the gradual decline in rate of waning, and the irregular nature of the curves.

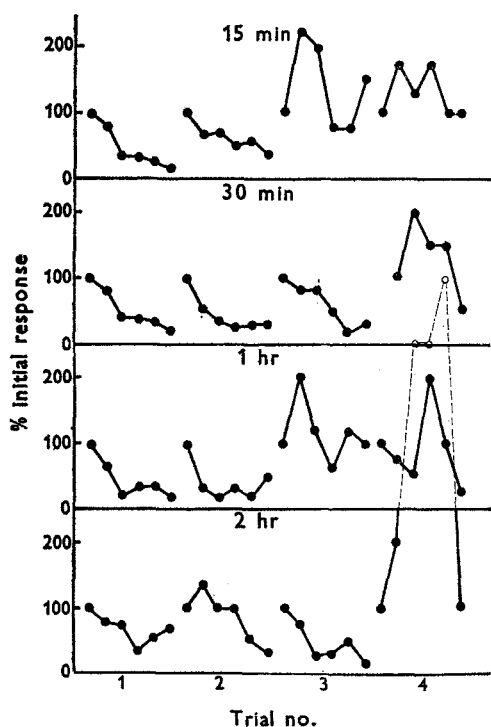


Fig. 10. The same data, for the first four trials, presented in relative terms; there is no evidence that waning is getting faster.

fluctuations of this order as 'anomalies' or 'noisy' data.

In Fig. 10 the waning is expressed in relative terms: the number of strikes within a session is shown as a percentage of the initial strike-level for that session. The irregular course of the waning is now even more apparent; only the first four sessions are shown, for after this the initial level of striking is so low that it is misleading to use it as a basis for a comparison in percentages.

There is certainly no evidence that the waning rates over the first four trials, however measured, are getting progressively faster; they appear to be about the same if measured relatively, or slower if measured absolutely. And over the last four trials it is difficult to see clear signs of any waning at all. Therefore, although a response may wane overall during repeated presentations, the rate of waning during individual presentations does not necessarily improve. This is at variance with one of Thompson & Spencer's (1966) 'parametric characteristics' of 'habituation' (see Discussion).

Finally, if the latency-time to the first strike in a trial is plotted as a frequency diagram, it is at once clear that, as the rate of striking decays, the latency to attack tends to increase (Fig. 11). Fewer animals attack; and many of those that do attack more slowly. During the first three trials most animals attack at once (i.e. in less than 10 s) but thereafter the histogram becomes irregular, except that more and more animals cease striking altogether. In the histogram, data from all four interval times are pooled, as the length of interval had no effect on the pattern of latencies.

(7) **Stimulus specificity.** Obviously, the waning described here could occur for a number of

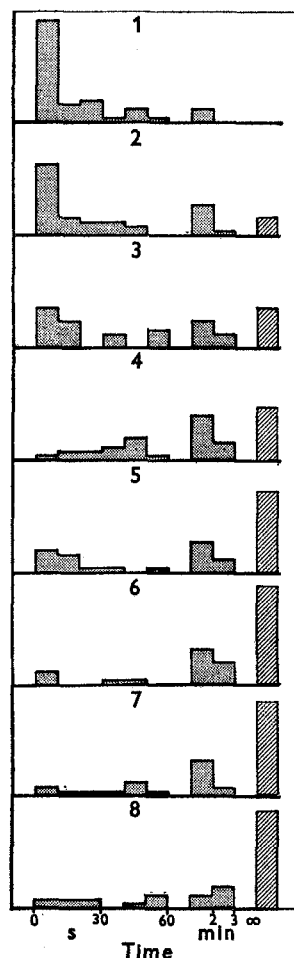


Fig. 11. Latency to first attack plotted as a frequency diagram (with intervals as indicated) for each of the eight trials ( $N = 40$ ). Note the steady increase, with experience, of non-attackers ( $\infty$ , stripes).



reasons, chief among them being motor fatigue or sensory adaptation; and it might not be specific to the stimulus.

To test for the last possibility we presented crabs to cuttlefish after their response to prawns had waned. This was done routinely after a second presentation of prawns [for reasons of economy these animals had to participate in another experiment (Section III, 1) that measured the recovery of the response after the prawns had been removed, and we wished to disturb the animals as little as possible. Pilot experiments presenting the crab after the first presentation gave exactly the same results].

Cuttlefish that were shown either a crab in a tube or a free crab (*Carcinus maenas*, about 45 mm carapace-width) after the tube of prawns had been removed nearly always attacked this crab within a few seconds. Indeed, we made it a criterion of the experiment that a cuttlefish that had been tested had to attack a crab within 3 min. If it did not it was discarded from the experiment and its results do not contribute to the present analysis: this happened in less than 2 per cent of cuttlefish tested. Thus the waning considered in this experimental situation is stimulus-specific.

Now although cuttlefish generally seize crabs with their arms they may strike at them with the tentacles (Boycott 1958). This was true also in this experimental situation; about a quarter of the animals caught crabs with the tentacles so that for them at least it was evident that failure to attack prawns was not the result of local motor fatigue. Although we cannot say this for the animals that caught crabs with the arms we can note that their arms were manipulated swiftly and efficiently and that all their other motor responses suggested that they were in excellent physical condition.

The behaviour of cuttlefish during testing with prawns also speaks against sensory adaptation as contributing largely to the waning process. It was rare for a cuttlefish to cease all attention activities towards the end of the test period and, notably, binocular fixation persisted, or frequently reappeared if it had momentarily stopped. Generally too, positioning was maintained (Fig. 2) and since this depends on visual feedback (Messenger 1968), here is further evidence that there is little or no sensory adaptation involved in this waning.

The time characteristics also support this conclusion: we are dealing here with minutes rather than seconds and it will be shown in later

experiments that although there is some recovery of the response after it has waned this is only partial, so that the effect of the process is relatively 'permanent'.

## II. The Effect of Reinforcement on the Waning of Striking

The waning process that we have been describing is more likely to be 'associative learning' than 'habituation', as those terms are defined by Thorpe (1963), for the animal presumably receives strong negative reinforcement as its tentacles strike the glass. Sometimes the tentacles are ejected with such force that the glass tube rocks on its base as it is hit by the terminal clubs. These clubs bear numerous suckers containing receptors of two or three types, including 'tension-receptors' (Graziadei 1959, 1964) and since each sucker contains at least 600 touch-receptors (Graziadei 1964) there is no doubt that the two tentacles are potentially capable of delivering 'pain' messages to the brain. Because it was important to establish that we were dealing here with 'associative learning', we tried to discover whether reinforcement affects the course and rate of waning. In this experimental situation negative reinforcement could be increased by giving the cuttlefish a small shock; it could be decreased by ensuring that the tentacles never struck the glass and to achieve this we surgically removed both tentacles.

In one series of experiments the cuttlefish was given a 10-V a.c. shock each time its ejected tentacles struck the wall of the tube. Two grey metal plates (about 15 cm square) were placed at each side of the tank so that when the cuttlefish moved into position (Fig. 1) it lay between these plates, which were 30 cm apart. The experimenter closed the circuit by a hand-held switch and opened it at once (i.e. shock duration was about 0.5 s). The plates were introduced very slowly by hand immediately prior to the introduction of the tube.

In another series of experiments the tentacles were removed under 1 per cent urethane anaesthesia: each tentacle was pulled fully out of its sac with forceps and cut off as close as possible to its base. (Where it was possible to make post-mortem examination, much later on, it was found that there was never more than a 5 mm of stump left inside the sac). This simple operation was completed in less than  $\frac{1}{2}$  min and the animals always recovered and swam about within 1 or 2 min. Control animals were an-

aesthetized only: there was no evidence that this had any effect on their behaviour.

**(1) The effect of shocking on the general behaviour ( $N = 10$ ).** The introduction of a pair of large metal plates in no way modified the attacking behaviour of a cuttlefish to a prawn, providing the plates were not reflecting. [If they were, then male cuttlefish would display at their reflection (Boycott 1958; Messenger 1970) and feeding behaviour would be abandoned.] The plates were so sited that the cuttlefish had to remain between them while positioning for the strike, but control animals, between plates that never passed current, behaved exactly like animals presented with a tube of prawns alone. There was no evidence that experimental animals associated the plates with the shock and became less responsive because of them. If the circuit was closed, however, and a potential of about 10-V. a.c. applied across the plates the animal instantly paled and jetted violently backwards, with the fins folded down and the head retracted, features normally associated with the fast escape reaction mediated by the giant fibres (Boycott 1958, 1961). The cuttlefish then paused for a few seconds, maintaining attention and darkening intensely, and then re-positioned itself between the plates for another strike at the tube.

Pilot experiments showed 10 V to be the most suitable size of shock. At potentials as low as 4 V the animal merely 'flinched', paling very slightly and retracting the head; higher voltages could produce ink ejection. There was no evidence that repeated shocking at 10 V had any permanently deleterious effect on the cuttlefish, which always fed normally when it was allowed to.

**(2) The effects of tentacle removal on the general behaviour ( $N = 28$ ).** The effect of tentacle removal is much more interesting. The animal makes an excellent recovery from such a simple operation: there are no motor defects or aberrations of posture or chromatic behaviour and attacks on prey animals may follow at once. Sexual behaviour appears unaffected and the animals may survive in the laboratory for weeks as long as they are fed on crabs or other slow prey that can be caught with the arms (Boycott 1958; Messenger 1968). For the one defect of these animals is the obvious one that without tentacles they are virtually incapable of capturing prawns or small fish, although sometimes these are caught by chance (the prawn's

escape-flip may take it into the arms of the cuttlefish).

The absence of tentacles, however, does not prevent the cuttlefish going through all three phases of the attack when it is confronted by a prawn. Attention and positioning occur as in intact animals (Messenger 1968) but seizure is now marked by a slight splaying of the arms and by the very short forward 'jerk' that an intact animal makes when its tentacles are ejected. This jerk is quite obvious and can be used as a measure that the last phase of the attack has been initiated, but it leaves the animal some centimetres away from the tube, so that in such a 'pseudo-strike' no part of the cuttlefish touches the tube. The attack sequence, then, terminates without any food reward, but equally without any 'pain' input from suckers on the tentacles. In these circumstances the animal pauses for 1 or 2 s and then makes another pseudo-strike; another pause is followed by another pseudo-strike and so on. Gradually the changes in colour, which often occur at this stage of the response (Messenger 1968) become intensified, and deep 'blushing' or total expansion of the chromatophores (Boycott 1961) occurs all over the arms, head and body. Often the animal swims round the tube at the attacking distance changing colour and making repeated pseudo-strikes. To anticipate the results somewhat, the level of attack by a cuttlefish without tentacles is so high that it is clear that such an animal cannot appreciate that it has no tentacles (see Discussion). This rather bizarre behaviour is not reserved for prawns in a tube: free prawns are pursued all over the tank without success.

**(3) The effect of reinforcement on the level of attack ( $N = 50$ ;  $N = 20$ ;  $N = 9$ ).** Ten animals without tentacles ('no tentacle' group) and ten animals that were shocked ('shocked' group) were exposed for 20 min to prawns in a tube. Their response to the stimulus altered during this time and the number of strikes (or pseudo-strikes) they made in a given time began to diminish so that we could compare their behaviour in this situation with that of thirty unoperated, unshocked animals ('intact' group: Section I, 3). Consider Fig. 12, which plots the mean number of strikes, in 5-min blocks, over a whole 20-min presentation. It is apparent from this that reinforcement has a critical effect on the level of striking throughout the test period. Shocked animals always attacked

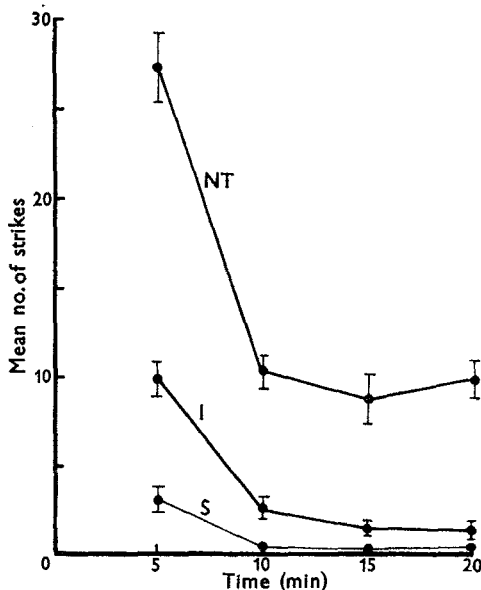


Fig. 12. Absolute waning of seizure during 20 min continuous presentation, plotted in blocks of 5 min. Bars indicate SE of mean. NT, no tentacles ( $N = 10$ ); I, intact ( $N = 30$ ); S, 10-V shock ( $N = 10$ ).

less than intact ones; and these always attacked less than no-tentacle animals. Indeed, these latter attack so frequently that during the last 5 min of presentation their attack-level is not significantly different from that of intact animals during the first 5-min period ( $t = 0.19$ ,  $df = 38$ ,  $P > 0.05$ ). The high level of striking by the no-tentacle animals, which was abundant proof that the operation itself had no general deleterious effect, was remarkable: in the first 5 min it was nearly three times the level of intact animals and about seven times that of the shocked animals. This emerges equally clearly if we break down the performance during the first 5 min into 1-min blocks as is done in Fig. 13. Here we can see how shocked animals stopped attacking after 2 min while intact animals continued to make a few strikes, though far fewer than no-tentacle animals, which, in the first minute, made over three times as many (pseudo) strikes as were made by the intact group. And during the last minute their attack-level was not significantly different from that of intact animals during the first minute ( $t = 0.22$ ,  $df = 38$ ;  $P > 0.05$ ).

To confirm that tentacle-removal heightens the attack-level we tested another group of ten animals in a series of repeated 3-min presenta-

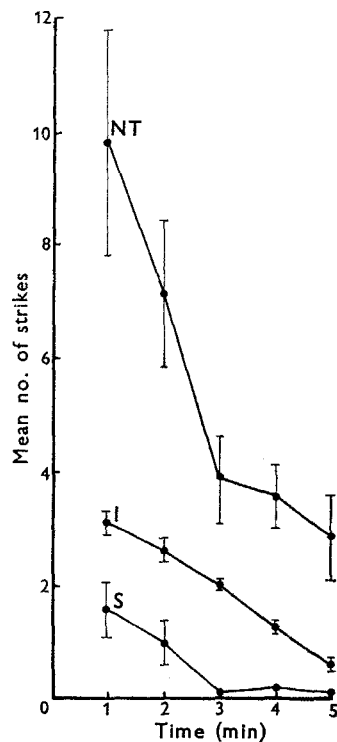


Fig. 13. The same: the first 5 min, plotted in blocks of 1 min. Conventions as before.

tions at intervals of 30 min, comparing them again with ten 'intact' animals (from Section I, 4). The results are shown in Fig. 14. Initially, the no-tentacle group attacks much more ( $t = 7.90$ ,  $df = 18$ ,  $P < 0.001$ ) and it continues to make significantly more attacks, trial by trial, than the intact group throughout training. However, the final level of attack by no-tentacle animals is significantly lower than the initial level of attack by intact animals ( $t = 3.329$ ,  $df = 18$ ;  $P < 0.01$ ) so that evidently with repeated presentation there is a more rapid waning of striking, in absolute terms, than with continuous presentation. The significance of this is not clear.

All the experimental manipulations described here affect the level of negative reinforcement, sometimes augmenting it (shocking), sometimes reducing it (removing the tentacles). None of these groups receives positive reinforcement. Suppose we were to offer such reinforcement by giving a food reward for every few strikes made on the tube? This was done with a small group of cuttlefish ( $N = 9$ ) with the predicted result;

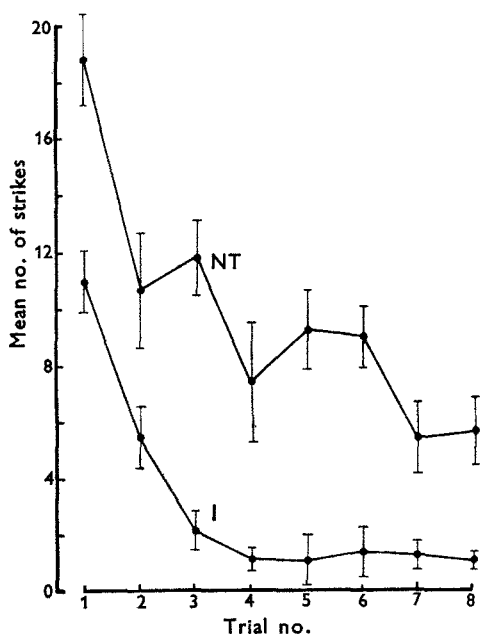


Fig. 14. Absolute waning during repeated presentation (3-min trials, 30-min intervals). Bars indicate SE of mean. NT, no tentacles ( $N = 10$ ); I, intact ( $N = 10$ ).

attacks on the tube persist. In practice, we put a freshly-killed prawn directly into the arms of the cuttlefish after it had made five strikes. The prawn was taken and eaten, which took 2 or 3 min; during this time the cuttlefish remained fixating the prawns in the tube, while staying in position, and when it had finished eating attacked again. After five further strikes another reward was given and the same pattern of behaviour ensued. All cuttlefish persisted in attacking, eating, pausing and re-attacking until they had eaten three to four prawns in a 20-min period, at the end of which they were still attacking. Because of the time spent in eating, these cuttlefish did not make significantly more attacks per 20 min than unrewarded animals, but two cuttlefish that were allowed to go on attacking prawns in a tube for 40 min made no less than thirty-five and thirty attacks in this time and were fed seven and six prawns respectively. Cuttlefish rapidly become satiated on prawns (Messenger 1968), so that it was not profitable to pursue this experiment, especially as the predicted result was obtained. Presumably one could continue to elicit attacks on prawns in tubes for ever by feeding for attacking the tube. The point is that, before satiation effects behav-

iour positive reinforcement increases the strike level.

(4) **The effect of reinforcement on the rate of waning** ( $N = 50$ ;  $N = 20$ ). The level of attack by cuttlefish on prawns in a tube is obviously greatly altered by the amount of negative reinforcement the animal receives, but we must now consider whether reinforcement affects the rate of waning of striking.

It is important to be clear about how rate of waning is measured, for as Hinde (1970) has pointed out this will determine the result. So far we have been talking in absolute terms: the slopes in Figs 12 to 14 all show the absolute response decrement. From Fig. 12 it appears that, in the initial phases, learning proceeds slower as negative reinforcement increases and Fig. 13 supports this idea in as much as the waning of the response in no-tentacle animals is clearly fastest in the first 2 min. (The significance of the sharp change of rate after the third minute is not clear.) During repeated presentation (Fig. 14), however, it looks as if the level of negative reinforcement does not greatly affect the rate of waning in absolute terms.

Yet because it affects the level of attack reinforcement level will alter the relative rates of waning. If we choose to plot the performance during continuous presentation as a percentage of the initial level (Fig. 15) we find that the response wanes faster as negative reinforcement increases, which is what might be expected.

(5) **The role of the motor command in learning** ( $N = 70$ ;  $N = 8$ ). The experiments with no-tentacle animals show that the response wanes in the apparent absence of reinforcement but they do not exclude the possibility that efferent copy of the motor command is used as a basis for learning or the possibility that there is feedback from receptors in the 5 mm stump of tentacle left in the tentacle-sac after its removal. Can learning proceed in intact animals when the tentacle is prevented from being ejected? To test this we took advantage of the fact that a cuttlefish only ejects its tentacles at prey when it has reached the attacking distance (Messenger 1968). To prevent it attaining this we placed a clear Perspex screen ( $30 \times 50$  cm) across the tank and introduced the tube of prawns behind this so that the screen-tube distance exceeded the attacking distance (Fig. 16B). In these circumstances the cuttlefish shows attention in the normal way but as it swims to get into position it encounters an invisible barrier; it

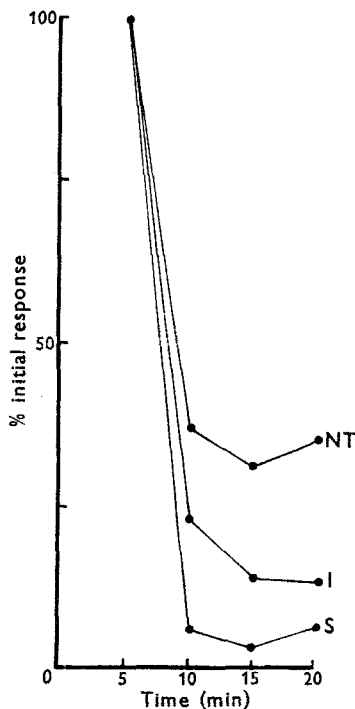


Fig. 15. Relative rates of waning during continuous presentation (cf. Fig. 12). Scores (per 5-min block) are expressed as a percentage of the first 5 min. Abbreviations as before.

swims against this for some time, gently rubbing its arms against the screen, often becoming very dark and showing waves of intense chromatic activity. Most animals in the experiments spent the whole of a 3-min trial-with-screen 'swimming on-the-spot' towards the prawn in a tube, which remained out of reach. Both attention and positioning are maintained, then, and for as long as the screen is present cuttlefish do not initiate the final motor act of the attack: the tentacles are never even partially ejected.

In practice, we ran three groups of animals ( $N = 20$  each) in a series of eight, repeated, 3-min presentations at intervals of 30 min, while a fourth group ( $N = 10$ ) (from Section I, 4) acted as a control. The control group was always allowed access to the tube, but the others were screened off from it for two, four, or six trials and then allowed access (for six, four, and two trials respectively). The results are shown in Fig. 17: it is apparent that there are no differences in the initial level of striking of the four groups (analysis of variance,  $F = 1.15$ ;  $df = 3, 66$ ;  $P > 0.05$ ), nor in the rate of waning in the early

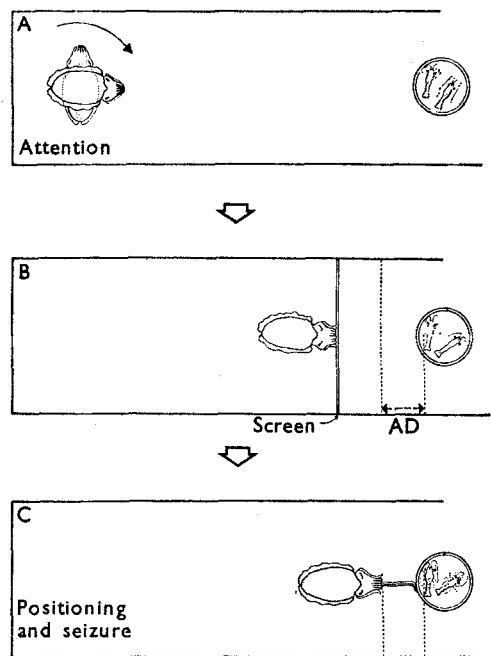


Fig. 16. The experimental situation when a screen is interposed to prevent the *Sepia* gaining the attacking distance (AD). Removal of the screen is followed rapidly by positioning and seizure.

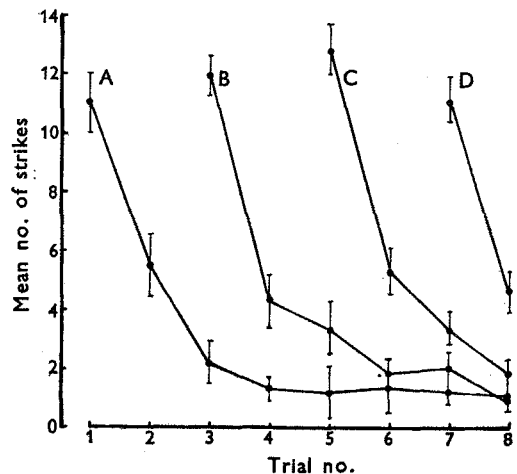


Fig. 17. Absolute waning during repeated presentation with screen (3-min trials, 30-min intervals). A, control group, all trials with access ( $N = 10$ ); B, first two trials with screen ( $N = 20$ ); C, first four trials with screen ( $N = 20$ ); D, first six trials with screen ( $N = 20$ ). Bars indicate SE of mean.

stages. In other words, cuttlefish that have been exposed without access to prawns in a tube for as long as 18 min (group D; six trials of 3 min each) make just as many strikes when they first attack as animals that have never seen prawns in a tube before (group A). Furthermore, the amount of visual experience has no effect on the level of attack during the second trial with access (analysis of variance,  $F = 0.44$ ;  $df = 3, 66$ ;  $P > 0.05$ ).

If we compare the results of group D (six trials without access; two trials with access) with those from no-tentacle animals (allowed eight trials with access) it is at once clear (Fig. 18) that cuttlefish learn more by 'pseudo-ejecting' tentacles that they do not possess than by *not* ejecting tentacles that they do.

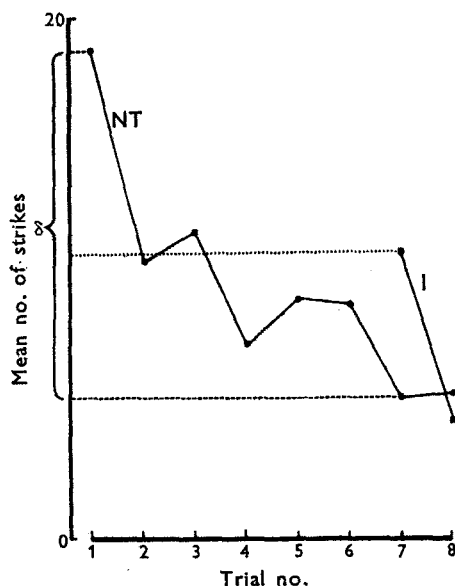


Fig. 18. The effect of motor experience. Before trial 7 both groups have had 18-min visual experience. One has been allowed access to make pseudo-strikes (NT), the other denied access and prevented from striking (I). Change in strike level over seven trials is indicated on the ordinate for the NT group (8); for the I group it is effectively zero (cf. Fig. 17)

This finding was confirmed with a small group of animals ( $N = 8$ ) all of which had the tentacles removed. Half the group were allowed access to the tube for all eight trials, the other half for four trials. The result was the same: on the first trial with access to the tube (i.e. trial number 1 or number 5) the levels of pseudo-strikes were no different ( $t = 0.285$ ,  $df = 6$ ,  $P >$

0.05). Learning does not commence until the final motor act can be initiated.

### III. The Recovery of a Response that has Waned

It has been shown that cuttlefish presented with prawns in a glass tube stop striking at them after a short time, and that this is at least partially the result of the negative reinforcement ('pain') derived from the tentacles as they hit the tube. The waning of the response that occurs in the experimental situation evidently represents some kind of learning, probably 'associative learning' (Thorpe 1963). How long does such learning persist? If we remove the stimulus for a time and then replace it does the response recover to its former strength? Or does that depend on the length of interval between the first and the second presentation? If so, what is the nature of the recovery curve? Does the recovery of the response after a fixed interval depend upon the length of the first presentation? And does recovery depend upon the level of negative reinforcement received during 'training'? These experiments attempt to answer some of these questions but they provide only one clear conclusion: the course of recovery of the response after it has waned is complex and irregular and is almost certainly the result of more than one process. In this our experiments support the thesis of Hinde (1954, 1960, 1970), though our interpretation of the results is somewhat different from his. A preliminary account of some of these experiments has been made before (Messenger 1971).

(1) **Recovery as a function of rest-interval** ( $N = 222$ ). The form of this experiment was as follows. A tube of prawns was shown continuously to a cuttlefish for 20 min (initial presentation). It was removed for a rest-interval, during which the cuttlefish remained unfed, and then replaced for 5 min (second presentation). The length of the rest-interval varied from 2 min to 2 days (Table I). We recorded the number of strikes in the first 5 min of the initial presentation (*a*) and the number in the second presentation (*b*); and calculated the 'recovery score' for that individual from the ratio

$$\frac{b}{a} \times 100$$

It is important to make quite clear the implication of this way of expressing recovery: if an animal made no strikes the second time (in practice this was quite common) its score would be zero or, in another terminology, it would

show 'perfect retention' ('100 per cent savings'); if it made the same number of strikes on the second occasion its score would be 100 or, alternatively, it would show 'zero retention' (see Discussion).

Group performances could be estimated by taking means of percentage scores in the usual way, but to permit parametric statistical operations with ratios we used the mean of arcsin-transformed individual scores (Bishop 1966).

The effects of fourteen different rest-intervals were examined eventually; fewer intervals were tested at first but unexpected irregularities in the recovery curve that appeared early in the collection of data forced us to introduce tests at other intervals and to enlarge existing groups until we had no less than twenty animals per group over what appeared to be the critical intervals of 22 to 90 min and fifteen per group for the others. Cuttlefish were allotted to treatments randomly.

On analysing all the results we encountered eight animals (out of 230) that had made more strikes on the second presentation than on the first. Because this was highly unusual, and because it could make a large difference to the group score, we decided to reject the results of these animals. This explains the discrepancies in the final numbers of animals in Table I, which sets out in summary the results of the whole experiment.

The results are represented graphically in Fig. 19: the most arresting feature of the recovery curve is that it is not even approximately smooth. Recovery is evidently not a single process, increasing linearly with time or as a rectangular hyperbola negatively accelerating;

it is a complex phenomenon depending upon at least two processes. True, recovery values are low after intervals of a few minutes and high after two days, but the steep dip in the curve at 60 min represents a statistically significant result that merits closer examination. Let us consider the graph in detail.

At first the response begins to recover with time (the animal 'forgets' as it were) yet after about 20 min recovery deteriorates (the animal appears to start 'remembering': the terms 'forgetting' and 'remembering' are used in a crude operational sense only and must not be taken to imply a single underlying process). From 30 to 45 min there is an apparent improvement in recovery but the values at these two intervals are not significantly different so this change represents a random fluctuation. Recovery deteriorates again after 45 min until after 60 min it is close to zero. At this point the animals are effectively showing perfect retention. This is the paradox of our results. *Cuttlefish express better retention of the stimulus-situation after 60 min than after 22 min.* After this there seems to be a relatively rapid increase in recovery ('forgetting' again increases) to a steady level that is reached after 1½ hr. The slight decrease in recovery-score at 8 hr and at 1 day (Table I) is not statistically significant.

It is noteworthy, incidentally, that the response never recovers to much more than a quarter of its initial value so that a 20-min experience of attacking prawns in a tube is ample for very high retention indeed, even 2 days later.

In Fig. 19 results are also plotted after arcsin transformation to show the standard errors of

Table I. Recovery as a Function of Rest-Interval (14 treatments; total  $N=222$ .)

Rest-interval	2 min	4 min	8 min	15 min	22 min	30 min	45 min	60 min	90 min	2 hr	4 hr	8 hr	1 day	2 days
$N$	15	15	15	15	20	19	20	19	17	14	15	14	14	10
Mean strikes, first presentation*	8.8	9.3	10.5	11.4	13.3	12.5	11.5	11.7	13.9	10.1	10.7	11.3	13.2	12.6
Mean strikes, second presentation†	0.4	0.1	0.4	0.5	3.0	1.6	2.1	0.4	3.8	2.0	2.8	2.1	2.9	4.0
Mean % recovery	3.6	1.6	4.1	6.5	22.9	12.5	19.3	2.9	27.6	23.0	27.5	15.7	16.7	30.0
Mean % (arcsined)	0.5	0.3	1.1	2.4	16.1	4.9	11.1	0.6	21.6	14.1	20.8	10.1	10.1	22.1
SE mean	0.25	0.09	0.23	0.36	0.68	0.64	0.75	0.14	1.10	1.00	1.35	0.56	0.65	1.60

\* $F=1.45$ ;  $df=13, 208$ ; NS.

† $F=3.9$ ;  $df=13, 208$ ;  $P<0.001$ .

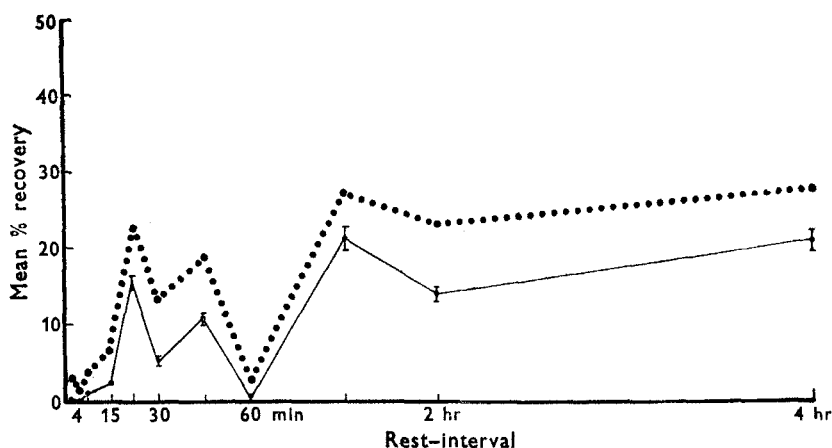


Fig. 19. Recovery after rest-intervals of up to 4 hr (cf. Table I). The dotted line plots the means of untreated data. The other line shows the means of arcsin-transformed scores that have been re-transformed into percentages; bars show SE of mean, but are not drawn where this is too small.

the means; with data in this form it is possible to run *t*-tests and analyses of variance for unequal sized sets and when this is done the following points emerge:

(1) Recovery is not statistically different after the rest-intervals: 2, 4, 8, 15, 60 min ( $F = 0.70$ ;  $df = 4, 74$ ;  $P > 0.05$ ).

(2) Recovery is not statistically different after the rest-intervals: 22 min, 90 min, 2 hr, 4 hr, 8 hr, 1 day, 2 days ( $F = 0.49$ ;  $df = 6, 97$ ;  $P > 0.05$ ).

(3) For the six intervals over the critical part of the curve (15, 22, 30, 45, 60 and 90 min) analysis of variance shows there is a highly significant difference between the variation among treat-

ments and the variation within them ( $F = 3.85$ ;  $df = 5, 104$ ;  $P < 0.01$ ).

(4) The recovery score after 60 min is significantly poorer than it is after 22 min ( $t = 3.71$ ;  $df = 37$ ,  $P < 0.001$ ) or after 90 min ( $t = 3.65$ ,  $df = 34$ ;  $P < 0.001$ ).

Finally, we can simply consider the level of strikes during the second presentation (Fig. 20). This gives us essentially the same graph as before, with the dip at 60 min, and that this irregular curve embodies significant differences is shown by analysis of variance: there is a highly significant difference ( $P < 0.001$ ) between among-treatment and within-treatment scores (Table I). Clearly the length of rest-interval has

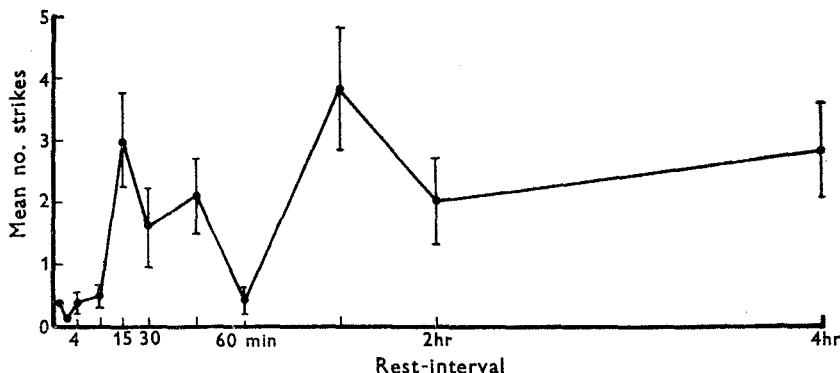


Fig. 20. The effect of rest-interval on strike-level during second presentation; bars indicate SE of mean.



influenced the strike-level on the second presentation. (There was no significant difference between strikes made by different interval groups during the first presentation: see Table I.) Furthermore the mean strike-level of animals tested after 60 min is significantly lower than that of animals tested after 22 min ( $t = 3.28$ ,  $df = 37$ ,  $P < 0.01$ ) or after 90 min ( $t = 3.29$ ,  $df = 34$ ,  $P < 0.01$ ).

Taken together these findings suggest that the 'dip' in the recovery curve at about 1 hr after the end of first stimulus-presentation is a genuine product of the experimental manipulation: whatever the interpretation (see Discussion) the recovery of the striking response after it has waned is a complex process that occurs in at least two phases.

**(2) Recovery as a function of length of initial presentation ( $N = 50$ ).** The extent to which a response that has waned will recover after a fixed interval is likely to depend on the duration of the first stimulus presentation: if it is very brief we would expect recovery to be greater than if it is prolonged. To verify this we took another group of naïve cuttlefish and showed them prawns for either 2, 4, 8, 15 or 30 min ( $N = 10$  each treatment). At the end of presentation we removed the tube of prawns for 24 hr. It was then replaced for a further period of 2 min. If the number of strikes made in the second exposure is plotted against the length of the initial exposure (Fig. 21) it is clear that, despite slight irregularity, fewer attacks are made after longer exposures, i.e. there is an inverse relationship between strike level (hence, recovery) and length of initial presentation. Analysis of

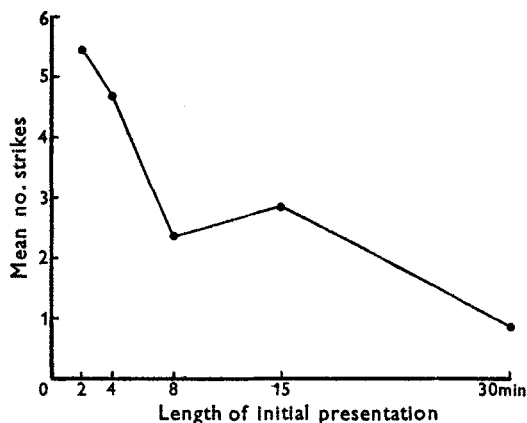


Fig. 21. Strike-level during second presentation as a function of length of first presentation.

variance shows that the difference in strike-levels between the groups is significantly greater than it is within them ( $F = 3.04$ ;  $df = 4, 45$ ;  $P < 0.05$ ).

This experiment also provides important evidence that motivation is unlikely to be contributing greatly to performance during second presentation. All animals could be considered equally hungry after 24 hr without food yet some attacked much more often than others: these were all animals with less experience of the stimulus situation.

**(3) Recovery after a fixed interval from a series of repeated presentations ( $N = 40$ ).** In an earlier experiment (Section I, 4) we compared the course of waning during repeated presentations at varying intervals. The animals were all shown the prawns in a tube for eight 3-min trials but these were separated by an interval of either 15, 30, 60 or 120 min ( $N = 10$  for each treatment). During this time the strike response waned (Fig. 8) but when, 24 hr later, the stimulus was shown again for 3 min the response recovered equally in all four groups and, as might be expected, there was no significant difference in the mean strike-level on this retention trial between groups trained at different intervals ( $F = 0.421$ ;  $df = 3, 36$ ,  $P > 0.05$ ). The mean recovery score, incidentally, was 18 per cent, which agrees well with the value obtained 24 hr after continuous presentation (Table I).

**(4) The effect of reinforcement on the recovery of the response ( $N = 30$ ).** It has been shown that cuttlefish deprived of their tentacles continue to make frequent attacks on prawns in a tube, though such attacks cannot, of course, lead to the tentacles being thrown against the glass; the 'pseudo-strikes' that such animals make are equated here with strikes proper, and advantage is taken of this behaviour to compare response-recovery in cuttlefish that have learned with, and without, negative reinforcement.

Two groups of naïve animals were shown prawns in a tube continuously for twenty minutes; the tube was then removed and presented again 2 hr later for 5 min. Fifteen animals had both tentacles pulled out of their sac and cut off under anaesthetic; the other fifteen animals were merely anaesthetized and had the tentacles pulled out of their sac. If we compare the mean number of strikes in the first 5 min of the first presentation with the mean number in the second presentation, it can be seen

Table II. Recovery With and Without Tentacles

	Initial presentation (first 5 min)	Second presentation (5 min)	
Intact	17.00 ( $\pm 0.96$ )*	4.60 ( $\pm 1.36$ )†	= 27.06% recovery
No tentacle	23.20 ( $\pm 1.96$ )*	13.93 ( $\pm 2.19$ )†	= 60.04% recovery

\* $t = 2.90$ ;  $P < 0.01$ .

† $t = 3.61$ ;  $P < 0.01$ .

Figures refer to mean number of strikes (with SE of mean);  $df = 28$ .

(Table II) that on both presentations no-tentacle animals attack significantly more than intact animals. If we calculate the number of strikes in the second presentation as a percentage of the number in the first 5 min of the initial presentation, we find the mean recovery score is 60 per cent for no-tentacle animals but only 27 per cent for intact animals. Comparison of the recovery scores by  $t$ -test (after arcsin transformation) shows that this difference, too, is significant ( $t = 2.74$ ,  $df = 28$ ,  $P < 0.02$ ).

Evidently intact cuttlefish, which have had strong negative reinforcement, show much weaker recovery of the response 2 hr after a 20-min exposure to prawns in a tube, than do animals without tentacles, or, to put it another way, they express much more retention of the stimulus situation. This emphasizes again that recovery scores depend upon previous experience, including the level of reinforcement.

### Discussion

#### The Experimental Situation

These experiments involve a short sequence of natural behaviour, prey capture, and they exploit the fact that in cuttlefish this behaviour depends only on visual information (Sanders & Young 1940; Messenger 1968). All three phases of the attack are elicited by prawns behind glass so that evidently we are presenting the test animals with a situation that is biologically meaningful. Confirmation of this comes from the very low rejection rate of animals that had been initially selected, as well as from experiments in which cuttlefish have free prawns and prawns-in-a-tube together in the tank; in these circumstances the animals often continue to make unrewarded attacks on the prawns in the tube despite the presence of accessible prawns.

This effect can be enhanced by presenting large prawns in the tube and small ones outside.

The response itself could be termed an 'inborn' one. Although there is some evidence of maturation (e.g. decrease in latency to attention) the details of the response as they appear in newly-hatched animals are very similar to those found in the adults tested here; the accuracy of striking, for example, does not improve with experience (Wells 1958). Undoubtedly, however, experience plays a part in the feeding behaviour of an adult cuttlefish (Wells 1962), and the population sampled in these experiments must include individuals with quite different experience of prawns.

The chief criticism of the experimental design has already been mentioned: perfectly still prawns do not elicit as many strikes as moving ones, and some prawns move more than others. This is, of course, true in life but it does mean that, despite the 'jiggling' resorted to, the prawns were obviously not equal stimuli for all cuttlefish. Further, although every effort was made to choose similar prawns, they could differ slightly in size and colour as well as mobility and could be a relatively large prey for small cuttlefish though small for large ones. One way of overcoming these difficulties would be to project cine-film of a standard sequence of prawns swimming; this would be a difficult procedure under water, however, and it seemed doubtful whether it would materially alter our findings. Pilot experiments show that small differences in prawn size and colour are not matched by any differences in the behaviour of the cuttlefish. The other objections were met by standardizing the procedure as far as possible and by using large numbers of animals. There was, incidentally, considerable variation in strike level but the numbers of strikes made by individuals were normally distributed: they ranged from one to thirty-six per 5-min period, the median being ten.

The success of a behavioural experiment depends upon the extent to which the experimenter can prevent the animal 'getting round' the problem set. And some cuttlefish do produce an adaptive response in this situation that makes the interpretation of their behaviour very difficult: they switch to lunging the whole body at the tube, opening the arms as they do so, which is the kind of response usually reserved for slow prey such as crabs (Boycott 1958) or *Squilla* (Messenger 1968). Since a lunge is the

culmination of an attack sequence, we could equate it with a strike by the tentacles. Unfortunately, it is not always easy to be sure when one lunge ends and another begins, especially when the lunge takes the arms onto the tube, where they can spread out in a grasping movement. For this reason the lunge was not scored as a strike, and where an animal made more lunges than strikes its results were excluded from analysis. Only three or four animals out of hundreds behaved like this. Generally, the lunge was an occasional event, commoner towards the end of a presentation period.

### **The Waning of the Different Stages of the Response**

Perhaps the most arresting result of the experiments is not that the response wanes but that the three separate components of the response wane at different rates (Fig. 2). Seizure or striking wanes quickest, positioning more slowly, and attention the slowest of all, whether we consider waning relative to the initial level of response or in absolute terms. Qualitatively, this is also true of repeated presentation.

**Attention.** The first stage of the response, is a kind of 'orientation' process, and workers with several different species agree that this stage of a response wanes more slowly than later stages (Precht & Freytag 1958; Melzack 1961; Rodgers, Melzack & Segal 1963; Leyhausen 1965). Such behaviour is obviously adaptive: a potentially important situation must at least be kept under observation. In programming the attack the cuttlefish brain makes three major 'decisions': 'attend' or 'not attend'; 'position' or 'not position'; 'strike' or 'not strike'. The last is contingent upon the second and the second upon the first so that this is the most important decision of all. Only if there is the strongest evidence that the situation is unimportant can the animal abandon surveillance. And of course it is this phase which reappears first when the experimental situation is presented again on subsequent occasions (cf. Thompson & Spencer 1966). Indeed, the later phases sometimes never appear.

**Positioning** must occur before the cuttlefish can strike at the prey with its tentacles. This is obviously related to the length of the tentacles, but once the cuttlefish is in position with the prey binocularly fixated it can presumably better decide whether or not the prey is suitable for attack. Certainly this is a stage of the attack

that is often prolonged, perhaps for minutes, under more natural circumstances, so that it is not surprising to find it persisting here even after several strikes have brought no reward.

**Striking (or seizure)** is a different matter. The strike is a brief motor event that must involve a fair expenditure of energy and it is a programme that anticipates instant 'pay-off': the decision 'strike', made in the optic lobes (Young 1963) and executed via the interbasal lobes (Boycott 1961) predicts that the results-of-action-signal ('food'/'not food') will shortly arrive via receptors in the lips (Young 1963). There is, therefore, an important output-input relation acting here in the very short term. If the signal 'not food' arrives only once another strike will probably be initiated (prawns are not always caught first time even in the sea) but if it arrives repeatedly it is highly likely the decision system will modify its instructions to 'not strike'. We should therefore expect the striking rate to fall rapidly, as it does.

Because the strike represents the culmination of the attack it is clearly the best measure of the response of a cuttlefish to a prawn in a particular situation; in a sense the strike is the attack. For this reason, but also because it is a discrete event and so convenient to record, we restricted ourselves to a consideration of this event in most of the subsequent experiments. By so doing we obviously lost a lot of potential information that could have been obtained if details of attention and positioning had been measured with a multi-channel event recorder: the duration of arm waving and 'blushing', the latency to monocular then binocular fixation, the precise time spent in positioning, for example. It seems unlikely, however, that the general picture thus obtained would have been very different.

### **The Waning of Striking**

During continuous presentation the number of strikes per unit time wanes dramatically over a 20-min period, and especially over the first 5 min of that period, whether this is expressed relative to the initial level of striking or in absolute terms. It is noteworthy that over half the strikes made in a 20-min period are made within the first 3 min.

It is not surprising, therefore, to find that the latencies are very short; about half the animals make the first strike within 30 s but most individuals strike within the first 10 s of presentation. What is interesting is to find that the

maximum rate of striking is delayed slightly and not reached until the second period of 10 s (Fig. 4). A healthy cuttlefish requires no more than 3 or 4 s to come down the tank, get into position and eject its tentacles so that this is a substantial delay that may represent some kind of 'warm-up' period, a phenomenon known in many organisms at different levels of organization (for example, the withdrawal response of earthworms (Roberts 1966); the courtship movements of male sticklebacks (Sevenster-Bol 1962); the mobbing response of chaffinches (Hinde 1954); and several mammalian reflexes (Sherrington 1906)). We can only speculate, of course, on what exactly 'warm-up' means in terms of the cuttlefish nervous system.

So far we have been considering only continuous stimulus presentation but we have seen that when a cuttlefish is shown prawns in a tube in a series of repeated presentations, the course of overall waning in the level of striking is similar to that occurring during continuous presentation (Section I, 3 and 4). We cannot be certain of this, for the reasons set out above (Section I, 4), but the similarities in the time course of both decay curves are most suggestive; in both, the majority of strikes occur in the first 5 or 6 min, and in both the rate decreases sharply after about 15- to 18-min exposure to the stimulus (Fig. 6). By this time the rate of striking seems to be approaching a steady value.

What is more interesting is that the rate of waning during repeated presentation seems to be independent of interval length, at least with trials of 3 min and with the intervals chosen here, which varied from 2 hr to  $\frac{1}{4}$  hr. There are signs, however, that waning proceeds faster with massed trials than with spaced ones (Fig. 8) and this point needs to be fully resolved by an experiment using a larger number of animals.

In relative terms, of course, waning appears faster with continuous presentation (Fig. 7), especially in the early stages, because of the lower scores made by the continuous groups. The importance of distinguishing between these two ways of measuring waning has been emphasized recently by Hinde (1970) and is an especially important point when we come to consider the effects of waning during individual trials of a repeated series. When data for each trial of a successive series are examined and measured in terms of absolute strike-level it becomes apparent that the waning process is not as regular as it at first appears (Fig. 9). These findings provide further evidence for

Hinde's demonstration (1970) that the course of waning processes is not always smooth. When the first two or three trials are compared in relative terms it is clear that during these the rate of waning is about the same (Fig. 10). It is not getting faster. In absolute terms this must mean that the waning rate is actually getting slower and this is indeed hinted at in Fig. 9. Our point is that there is no evidence that the response is waning progressively faster in successive trials; rather the reverse.

Now Thompson & Spencer (1966) claim that 'habituation' becomes successively more rapid "if a repeated series of habituation training and spontaneous recovery are given". This 'parameter' of habituation has anyway been criticized (Hinde 1970) but there is another possible reason why our results do not conform to Thompson & Spencer's criterion: that we are dealing here not with 'habituation' but with 'associative' learning, a process that has different properties. This has been hinted at before and must now be considered in detail.

### The Interpretation of the Waning Process

In these experiments we have been dealing with the waning of a response to a specific stimulus under conditions where we can fairly confidently exclude sensory or motor fatigue as relevant factors. Because this waning involves the disappearance of a response it is at first sight tempting to see it as 'habituation'. Thorpe (1963) defines 'habituation' as the "relatively persistent waning of a response as a result of repeated stimulation which is not followed by any kind of reinforcement". The crux of the matter seems to be the reinforcement. Now we have seen that the level of striking is significantly lowered when negative reinforcement is enhanced and significantly raised when negative reinforcement is reduced (or when positive reinforcement is given). This is true of the first minute of presentation and remains so throughout the whole of a 20-min observation period (Figs 12 and 13). And, in relative terms, it is clear that the waning curve is sensitive to reinforcement level: learning proceeds at a faster rate as negative reinforcement increases (Fig. 15).

Because of this, it is suggested that the waning of the response of an intact cuttlefish to prawns in a tube cannot be 'habituation' but is, rather, an example of what Thorpe (1963) terms 'associative' learning. The tentacles striking the tube must deliver a 'pain' message to the brain and this pain is associated with the prawns

in the tube. It could be argued, of course, that we are dealing with a mixture of 'learning' and 'habituation' in the intact animals, which as well as getting negative reinforcement are getting no positive reinforcement: there seems no way of resolving this. By the same argument the waning exhibited by no-tentacle animals could be considered pure 'habituation'. We do not know, however, whether there is a pain input from the tentacle-stumps at every pseudo-ejection.

A case could also be made out that the waning of some phases of the attack, attention and positioning, are 'habituation' while the waning of striking is 'associative learning'. Yet if the waning of attention and positioning (in the absence of reinforcement) were both 'habituation' processes, then we might expect that their decay curves would be very similar one with other, though quite different from the decay curve of seizure. A glance at Fig. 2 reminds us that this is simply not true: curves for all three stages show a decremental process, negatively accelerating, but there is no obvious difference in kind between the curves, and they do not fall into two sharply defined categories. The crucial question, of course, is: does the neuronal basis for the waning of attention, or positioning, differ in kind from the neuronal basis for the waning of seizure? We suspect not, though we have no evidence about this yet.

The more general question is: at the cellular level does 'habituation' differ from 'learning'? At the moment we cannot say because we have no causal explanation of either. Because of this it is impossible to do more than speculate about a difference that may be largely semantic. Yet it might be more profitable for workers to address themselves to the similarities between apparently different types of adaptive changes in behaviour. How far, for example, is Horn's model of 'habituation' (1967) compatible with Young's (1965) theory of 'learning' or with Roberts & Flexner's (1969) model of long-term memory? Hinde (1954, 1960, 1970) emphasizes that it is not necessary to suppose that a single type of event underlines all waning processes, and of course this is true; but surely it is more economical at least to begin by assuming there is only one kind of process at the cellular level that underlies all Thorpe's types of learning? If this were so then the appearance in experiments of decay curves with different characteristics would result from different expressions of a single process, different because of the con-

nectivity of the cells involved or, perhaps, because of their different properties, which are both features that will have been selected for in evolution. On this argument each stage wanes at a characteristic rate because it has a different function rather than because it depends on a different underlying process.

To conclude: there are clearly difficulties in opposing Thorpe's categories of learning and even if there are fundamental differences between 'associative' learning and 'habituation' it seems unwise, even in operational terms, to apply these categories rigorously to changes in the different phases of the same response, as in the waning of attack in the cuttlefish. That response as a whole alters in the experimental situation and this alteration is stimulus-specific and adaptive so that it must be the result of some kind of learning. As Horridge (1968) would put it, cuttlefish that have stopped attacking inaccessible prawns behave 'as if they have changed some connexions between their nerve cells'. This change may or may not be what Thorpe terms 'associative' learning, but we have seen that the rate of waning of seizure is undoubtedly sensitive to the level of reinforcement.

### **Efferent Copy and the Sequential Control of the Attack**

By interposing a transparent screen between the cuttlefish and the tube of prawns we were able to elicit attention and positioning responses but prevent tentacle ejection (the screen is presumed to offer the minimum disturbance to the animal, which merely 'nuzzles' it very gently, and the persistence with which cuttlefish swim against the screen supports this contention). Under these conditions we find that cuttlefish learn nothing about the situation until they begin to eject their tentacles; then they learn as fast as, but no faster than, control animals (cf. the rates between first and second trial in Fig. 17). This is also true for animals without tentacles. Taken together these findings seem to imply that the initiation of the final motor is as important for learning as its execution. Figure 18 shows clearly that the strike-level wanes in animals without tentacles that are allowed to make pseudo-ejections, while it does not in intact animals prevented from making real ejections. So the command for the final 'consummatory' act of the sequence must be given if the animal is to learn that that act is an inappropriate one.

From Boycott's important study of the cuttlefish brain (1961) we know that the efferent pathway controlling tentacle ejection is:

optic lobe → interbasal lobe → anterior pedal lobe

but we do not have details of the afferent connexions of these lobes. Perhaps the cells in the optic lobe that initiate ejection at the end of the long and complicated attack sequence get feedback from the motor neurons in the anterior pedal lobe that they have executed the strike-command. This might somehow 'prime' the learning system, perhaps by starting the 'expectation of results' signals (Young 1963); such a system would operate even in the absence of tentacles. Unfortunately, however, we have no direct evidence that such efferent copy exists or is made available for learning. As we saw above, the waning of striking in no-tentacle animals could be an example of 'habituation' *sensu stricto* (Thorpe 1963). But, whether it is or not, it is certain that it does not develop until the last stage of the attack sequence is initiated.

These conclusions are unsatisfactory because they are so uncertain, but at least they remind us that in analysing an apparently simple behavioural response we may have to consider several factors, whose operation we only dimly perceive. For example, chaffinches (Hinde 1954) presumably have to start 'chinking' before they can begin to learn to stop. Perhaps efferent copy acts here, for, as Hinde (1960) admits, the role of reinforcement in the waning of chinking is not at all clear.

Finally, it is noteworthy that the introduction of a screen prolongs positioning and attention. We have seen before that these phases of the attack decay more slowly than the third phase, but in these experiments they never even began to wane. Does this mean that a motor sequence must run to completion before it can be switched off as inappropriate, or that one phase of the attack is not suppressed until the subsequent phase has been? The attack control system, in the optic lobes, presumably takes into account the sequential nature of the motor actions that make up the attack, thus ensuring that phase two persists until phase three has been shown to be fruitless and that phase one persists at least until phase two is abandoned. As we saw earlier this makes biological sense, but unfortunately we have no physiological evidence yet that the optic lobe contains populations of neurones with the different connexions that such a model demands.

### The Behaviour of Animals After Tentacle Removal

One of the most interesting findings in these experiments has been the discovery that after such an operation a cuttlefish cannot 'see' that it has no tentacles. Its behaviour to a prawn is like that of an intact animal and continues to be so right up to the very last moment. With a free prawn in the tank cuttlefish can be observed making sporadic pursuit movements for hours on end, moving all round the tank after an especially active prawn. This inability to take into account visually the position and attitude of a part of the body seems very curious by vertebrate standards, yet it may be the rule in cephalopods: squids and cuttlefish in aquaria frequently damage the end of the mantle by swimming into the wall of the tank, and in *Octopus* there is a very good evidence that proprioceptive information cannot be combined with the visual input to maintain eye orientation (Wells 1960). The behaviour reported here is all the more interesting because it must be possible for the cuttlefish to see the tentacle tip at the precise moment of seizure since the tip now occupies the place of the prawn that has been fixated previously. If further evidence were needed (Messenger 1968) that the tentacle-ejection phase of the attack relies on an 'open-loop' programme, we have it here. The strike-command is issued not only on the assumption that the prawn will not move but also that the tentacle will arrive at its target. The only way the cuttlefish seems to be able to tell if it did arrive is by waiting for signals from receptors in the lips, which can arise only after the prawn has been brought back into the mouth. This would account for the delay of a second or two before the animal initiates another strike.

Equally interesting is the fact that as cuttlefish grow the attacking distance and tentacle length both increase (there is strong positive correlation between them as would be expected: Messenger, unpublished observations). The growth rate of the tentacles is presumably related in a complex way to that of the eyes and head but it would seem that as the cuttlefish grows its eye has to assume its tentacle is the right length. That this is a reasonable assumption is shown by evidence that newly-hatched cuttlefish, those with some experience (Wells 1958), and adult animals (Messenger 1968) strike equally accurately. What would happen to a cuttlefish whose tentacles were injured naturally? This must be a comparatively rare

event, but on one occasion an animal with one normal and one very short tentacle was observed; the short one appeared to be regenerating. We would predict that were both tentacles shortened in this way their bearer would be unable to capture prawns.

Finally, it is particularly interesting that a cuttlefish, in a situation where it is persistently attacking yet failing to gain food, rarely switches over to its other mode of prey capture: the jump with arms outspread (Boycott 1958; Messenger 1968). Newly-hatched cuttlefish feed on prawn-like animals (*Mysis*, Wells 1958) that they capture with the tentacles. It seems very probable that they learn to make arm-attacks in young adult life, and that as such attacks will only be successful with slow-moving prey (crabs, *Squilla*) they will come to be restricted to them.

### The Two-Stage Recovery of the Response

When cuttlefish are exposed to the stimulus of an inaccessible prey-animal their response to that stimulus wanes. The number of strikes at prawns diminishes rapidly during a 20-min continuous presentation. Given that the response had waned we asked ourselves: how would it recover after a rest-interval? We anticipated that there would be little recovery if the stimulus was presented again 2 min later but that the response would recover almost completely 24 or 48 hr later. Our first unexpected result was that cuttlefish that have had 20-min continuous experience of attacking prawns in tubes attack very little on a second presentation, even 2 days later (Fig. 19). The waning of the response is therefore relatively permanent and this is further evidence that the changes we are studying are some kind of learning rather than fatigue or sensory adaptation.

The second surprising result was that the curve of recovery with time (Fig. 19) is not simple. Instead, recovery appears to depend on at least two processes, one that has reached its peak within minutes of the end of stimulation and has decayed by 22 min, and another that has reached its peak at 60 min. Despite the smallness of each group in statistical terms (there were never more than twenty animals per treatment) over two hundred naïve animals were tested in this experiment and we believe the results are a genuine reflection of different underlying processes. In particular, the difference in behaviour of the 110 animals tested at intervals of between 15 and 90 min show up as

highly significant, whether measured in terms of per-cent-recovery or in terms of mean-strike level.

The irregularities in the recovery curve could have arisen for a number of non-specific reasons, including differences in some environmental factor, such as oxygen-tension or nitrite-level, or because of the motivational state of the animal, for example 'fear' (though not hunger, see Section III, 2). Strictly speaking, these were not controlled for. Yet since there was a large turn-over of animals, occupying different tanks over a spread of time, such environmental differences (if they existed) would surely be lost, so that it is considered highly unlikely that this could be a source of the variation. It is not so easy to dismiss motivational factors, however, especially as we are very ignorant of the importance of these in cephalopod behaviour. It is possible that the 'dip' in the curve arises from the expression of fear, though it is not clear why such fear would take an hour to develop. And no aspect of the experimental situation appeared to be traumatic for the cuttlefish, although these are animals that readily show stress by ejecting ink and swimming violently (as, for example, when they are handled or netted). Finally, there is the argument that the curve is the (unconscious) product of the trainer's wishes: unfortunately, this cannot be refuted, for with a single experimenter it was not possible to test the recovery 'blind'. We can only say that the results obtained were counter to expectation, especially early on in the experiment! As far as possible we endeavoured to give all animals exactly the same treatment.

Given that the curve obtained is not the result of extraneous factors we must obviously ask ourselves how we are to explain it. Because we believe that the conditions of this experiment provide a conventional learning situation, it is tempting to see in the two-stage recovery curve the operation of two different memory systems, a short-term (STM) and a long-term (LTM) memory.

Consider the hypothetical situation in Fig. 22. Suppose that in *Sepia* there is an STM that rapidly builds up and decays fairly quickly. This memory could reach its peak within minutes of the last strike or, as cuttlefish often stop striking after only about 15-min exposure to prawns in a tube the peak could arise even before the end of the initial presentation. Thus, when the stimulus is presented again, 1 or 2 min after the end of the initial presentation, the

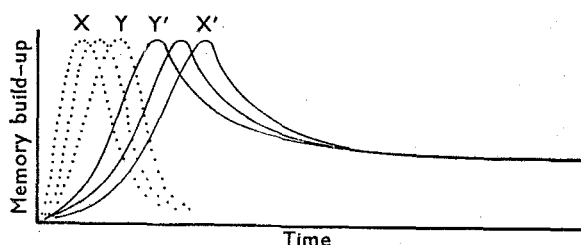


Fig. 22. A schematic representation of possible time courses of STM (dotted) and LTM (continuous). The peaks of these could shift under the influence of various parameters to reveal (X, X') or obliterate (Y, Y') the existence of the two separate memory systems.

STM would already be fully operative: this would explain the very low recovery after short-time intervals. We then have to assume a rapid decay in the STM to account for the recovery of the response during the first 22 min after stimulus-presentation (Fig. 19). Let us also suppose there is an LTM that develops more slowly, reaches its peak at about an hour after stimulus-presentation, and thereafter declines quickly at first and then very slowly. This would account for the almost perfect retention at 60 min and the 70 to 80 per cent retention at intervals of up to 48 hr. Finally, it is necessary to assume that the rate of build-up of both memory systems can vary slightly (Fig. 22). For one obvious objection to this explanation would be that if the STM and LTM systems in the cuttlefish are like those in other animals we would expect their effects to overlap in time. If, however, there is a certain latitude in their time-courses, depending, among other things, on the length of exposure to the stimulus and the amount of reinforcement received (cf. Section III, 4), the anomalous situation reported here of the STM decaying before the LTM has built up could arise purely as a product of the experimental situation. We may have separated, so to speak, the read-out of each memory system by a fortuitous combination of a suitable rest-interval with an appropriate length of stimulus-presentation, for there are two pieces of evidence that the latter has an effect upon recovery:

(1) When the interval between two presentations is fixed at 24 hr the recovery score is inversely related to the length of the initial presentation (Fig. 21).

(2) When we showed prawns for a 3-min trial and removed them for either 15, 30, 60 or 120 min before replacing them (Section I, 4; Fig. 8)

we found no differences in performance during the second trial ( $F = 0.44$ ;  $df = 3, 36$ ;  $P > 0.05$ ). Patently, if we had run our recovery experiment with an initial presentation of 3 min instead of 20 min, we would not have got the two-phase curve of Fig. 19.

Thus, the performance during a second presentation is likely to depend not only on the rest-interval after the first presentation but also on the duration of that presentation. We would predict, therefore, that were we to run the recovery experiment again with different lengths of initial presentation we might be able to shift the 'dip' in the recovery curve and perhaps make it either more or less obvious. With very short presentation lengths the dip would disappear and we should not artificially separate the effects of STM and LTM at all.

#### Short-Term and Long-Term Memories?

If the two-stage recovery really represents the activity of two memory systems we must ask how the time-course of these systems, as revealed here, agrees with what is known in other animals. In another cephalopod, *Octopus*, there are several pieces of evidence for STM (defined by a time-span of minutes) and LTM (defined by a time-span of days) although the problem of transition and interaction between these has attracted surprisingly little attention (but see Young 1964, 1970):

(1) LTM has been repeatedly demonstrated: two convincing examples are Sutherland's (1957) 27-day retention of a visual discrimination and Sanders' (1970) 120-day retention of a tactile discrimination.

(2) An LTM persisting for 2 to 3 days survives anaesthesia and electrical stimulation (Boycott & Young 1955).

(3) ECS can disrupt the read-out of memory 3 days later if it is given immediately after training though not if it is given 6 hr afterwards (Maldonado 1969).

(4) During a maze-running task that involves a delay an STM operates: delays of over 2 min lead to random performance (Wells 1967).

(5) The existence of an STM is implicit (a) in the finding that massed trials cause faster learning of a tactile discrimination than spaced trials, unless the vertical lobe is removed (Wells & Young 1969) and (b) in the demonstration that learning visual or tactile discriminations with delays of 15 or 10 s is impossible if the vertical lobe is removed although feasible



with 30-s delays if that lobe is intact (Wells & Young 1968).

These results are not at variance with ours. In *Sepia* we would claim that there is an LTM, which is fully established by an hour and which persists for at least 2 days, and an STM, operating at once but decaying rapidly in the first 20 min, at least under the experimental conditions specified here. Furthermore, taken together, these findings present a picture typical of many other animals, including mammals. Putting it as uncontroversially as possible, there seems to be a relatively stable, long-lasting process that is manifestly established by about an hour or so, and a more labile process that develops at once and persists only for a short time, of the order of minutes. The only other experiment in cephalopods addressed specifically to the problem of how these memory systems are related in time is that of Sanders & Barlow (1971, 1973). These workers trained octopuses not to attack crabs by giving them a 4-V a.c. shock for each incipient attack until they reached a criterion, of 1 min without attack. After varying intervals they retrained the animals in the same way and calculated retention scores. The retention curve they obtained bears a striking similarity to our Fig. 19 (or, strictly the inverse of it, for they expressed retention as mean-percentage-savings: see Section III, 1). It is not simple or monotonic: instead there are temporary reversals in retention and the curve seems to reflect the activity of more than one process. As they interpret it the curve is tripartite, reflecting the existence in *Octopus* of an STM, an 'intermediate memory' (IM) and an LTM (cr. Booth 1970).

What is interesting from our point of view is that the transition between their STM and IM occurs at a comparable time to the transition between the two stages of recovery reported here in *Sepia*. And furthermore, Sanders & Barlow present evidence that the presence and nature of the 'dips' in the retention curve is a function of strength of shock and length of training. As they put it "this suggests that the present results can be observed only within a limited set of training conditions" Sanders & Barlow 1971). This agrees precisely with the prediction made here for *Sepia*.

Finally, if we are right in our interpretation these results suggest that *Sepia* has two separate memory systems with parallel entry (Weiskrantz 1970). Shallice & Warrington (1970) have provided good experimental evidence that this is

what occurs in verbal memory in man; and the fact that a similar situation appears to occur in a group of animals so remote phylogenetically from ourselves, reminds us that many features of memory processes are likely to be universal.

**Note added in proof (October 1973).** Recent experiments suggest that learning in the experimental situation employed here requires that the vertical lobe system in the brain be fully developed. Where it is not, as in young *Sepia*, learning performance is significantly impaired.

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