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INHIBITION OF THE SWIMMING RESPONSE BY FOOD AND OF NEMATOCYST DISCHARGE DURING SWIMMING IN THE SEA ANEMONE *STOMPHIA COCCINEA*

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INTRODUCTION

The tentacles of a sea anemone are the sensory surface from which the animal obtains most information about the outside world, primarily from touch and chemoreception. One of the most characteristic reactions of the tentacles is the tendency to cling to objects that might serve as food. Undoubtedly this is due to a discharge of nematocysts. Some types of nematocyst discharge can be studied in isolated tentacles (Pantin, 1942). But some clinging responses of tentacles cannot be reproduced in isolation, e.g. the tendency of the tentacles of *Calliactis parasitica* to cling to shells (Davenport, Ross & Sutton, 1961). In that animal the nematocyst discharge in response to shell may trigger off the complex behaviour pattern by which the anemone transfers itself to the shell from another surface.

The remarkable swimming response of the sea anemone *Stomphia coccinea*, which was first observed by Yentsch & Pierce (1955), is also triggered by a specific response that may involve a nematocyst discharge. The tentacles of the anemone give this response to two species of starfish in the North Pacific, *Dermasterias imbricata* and *Hippasteria spinosa*, and to another in the North Sea, *H. phrygiana* (Robson, 1961*b*). The tentacles of *Stomphia* cling to these starfish as they do to food, but this leads not to the usual feeding response but to 'swimming'. Usually the anemone closes, then opens rapidly and bends or rocks violently from side to side, then sometimes within seconds it releases its pedal disk and finally 'swims' by continuing to make bending movements for some time afterwards.

Several authors have reported that when *Stomphia* is swimming in this way, it is quite unresponsive to handling and presumably to other stimuli to which it normally responds (Sund, 1958; Robson, 1961*a*). It seemed desirable to investigate this phenomenon further and in particular, to study the discharge of nematocysts to food and to *Dermasterias* at various stages in the swimming response.

METHODS

Tests were carried out by touching individual tentacles of *Stomphia* with pipe cleaners which had been dipped in an extract of *Pecten* or rubbed on the aboral surface of *Dermasterias*. Pipe cleaners proved to be more satisfactory for such tests than glass rods, which Pantin (1942) used in his studies on the nematocysts of *Anemonia sulcata*, probably because the cotton of the pipe cleaner absorbs and holds greater quantities

of material. The animals used were ten *Stomphia coccinea*, dredged from the San Juan Channel in Puget Sound near the Friday Harbor Laboratory. They were the same specimens used in our studies on electrical stimulation (Ross & Sutton, 1964).

As with our earlier work, on the responses of *Calliactis parasitica* to shells (Davenport *et al.* 1961) we found that individual tentacles of *Stomphia* could be touched by such objects without disturbing neighbouring tentacles. The nematocyst discharge of a tentacle is immediate and can be scored as '+' if the tentacle clings to the pipe cleaner, or '−' if it does not. Pipe cleaners direct from the package were used as controls. These were not absolutely ineffective (Table 1). Perhaps preliminary washing and sterilization of the pipe cleaners might be desirable if they are used in further work.

RESULTS

Local inhibition by food juices

The nematocyst discharge occurring in response to food material was tested with pipe cleaners dipped in the centrifugate from the ground-up muscles and gills from a half scallop, extracted in 8 ml. of sea water. Results of tests with this material are given in Table 1 and show the expected high proportion of '+' responses when 10 tentacles were tested at random. It can be presumed that this clinging response to

Table 1. *Numbers of tentacles sticking* ('+') *or not sticking* ('−') *to untreated pipe cleaners* (*controls*) *and to pipe cleaners dipped in centrifuge from* Pecten

Untreated controls		Treated with *Pecten* fluid	
+	−	+	−
9	91	93	7

Ten tentacles tested in each of ten *Stomphia*.

food is due to the discharge of nematocysts, though we did not follow this under the microscope. Most of our animals were small and their tentacles could not have been studied in isolation. Moreover, the specimens were being used for other experiments and we did not wish to damage them in any way.

Similar tests of the responses to pipe cleaners rubbed on the aboral surface of *Dermasterias* were carried out. To the eye the initial response appears to be the same as to food, namely, the tentacle clings to the pipe cleaner and it would seem that a discharge of nematocysts occurs. But the similarity of the two responses ends there, because this slight local contact with *Dermasterias* usually brings on the full swimming response of *Stomphia* within a few seconds. It was interesting to discover that touching a single tentacle with a material picked up by rubbing *Dermasterias* in this way could evoke the full swimming response. Previous work has shown that *Stomphia* is sensitive to small quantities of matter extracted from *Dermasterias* and poured over the tentacle in solution (Ward, 1962; Robson, 1961*a*). There has been no previous indication that the response could be evoked from such a localized sensory area as the tip of a single tentacle.

In some tests the *Pecten* extract happened to be applied just before the *Dermasterias* treatment. It was observed that the response to the active material from the starfish

was completely blocked under these circumstances. This phenomenon was studied more critically in two experiments.

(*a*) In one series of tests the whole tentacular crown was flooded with 0·5 ml. of the *Pecten* extract. For a short time afterwards, usually about 1 min., the tentacles failed to respond to pipe cleaners which had been rubbed on *Dermasterias*, and no swimming could be evoked.

(*b*) In the second type of experiment single tentacles of *Stomphia*, which could be identified because they occupied some distinctive position, were touched with pipe cleaners dipped in the *Pecten* extract. Tentacles so treated were then found to be unresponsive to *Dermasterias*. However, other tentacles, not touched by the pipe cleaner carrying the *Pecten* extract, were sensitive to *Dermasterias*; when touched by pipe cleaners rubbed on the starfish, they clung to these and almost at once, a swimming response developed. The photographs in Pl. 1 show how these experiments were carried out and illustrate the phenomena observed.

Table 2. *Local inhibition of nematocyst discharge and swimming response of* Stomphia (*to material rubbed off aboral surface of* Dermasterias) *by prior application of* Pecten *extract to the tentacular crown* (*tests* 1 *and* 2) *or to single tentacles* (*tests* 3 *and* 4)

Test	Treatment	Mode of application	Time (sec.)	Nematocyst discharge	Response of *Stomphia*
1	0·5 ml. *Pecten* extract	On tentacular crown	0		Tentacles withdrew slightly
	Dermasterias rubbing	PC on single tentacle	15	−	No swimming movements
	Dermasterias rubbing	PC on single tentacle	60	+	Pre-swimming movements
	Dermasterias rubbing	PC on single tentacle	120	+	Full swimming response in 10 sec.
2	*Dermasterias* rubbing	PC on single tentacle	Control	+	Full swimming response in 5–10 sec.
	0·5 ml. *Pecten* extract	On tentacular crown	0	.	.
	Dermasterias rubbing	PC on single tentacle	< 1	−	No swimming movements
3	*Pecten* fluid	PC on single tentacle	0	+	Nematocyst response only
	Dermasterias rubbing	PC on same tentacle	10	−	No swimming movements
	Dermasterias rubbing	PC on same tentacle	60	+	Full swimming response
4	*Pecten* extract	PC on single tentacle	0	+	Nematocyst response only
	Dermasterias rubbing	PC on same tentacle	5	−	No swimming movements
	Dermasterias rubbing	PC on same tentacle	10	−	No swimming movements
	Dermasterias rubbing	PC on different tentacle	15	+	Full swimming in 5–10 sec.

Stomphia no. 11. PC, Pipe cleaner.

It was found also that swimming could not be blocked by touching the tentacles with pipe cleaners dipped in the *Pecten* extract immediately after touching the same tentacles with *Dermasterias*. Attempts to apply both treatments simultaneously gave variable results. Perhaps, in spite of the apparently simultaneous application of the two treatments, sometimes the *Dermasterias* treatment, at other times the *Pecten* treatment, may have been applied earlier. This would mean that very short intervals of time might be important in determining which response takes precedence.

The procedure and the results of these experiments varied slightly according to the circumstances at the time. Table 2 shows information obtained from *Stomphia* 11 in our experimental group. The other nine animals gave essentially similar results.

It is clear that the swimming response to *Dermasterias* can be inhibited by the prior application of food material to the tentacles of *Stomphia*. This inhibition is peripheral and is located in the tentacles. We know this because a block set up in one tentacle does not affect the capacity of the *Dermasterias* treatment to evoke a swimming response on contact with another tentacle. Thus the neurones which co-ordinate swimming are not inactivated in any way.

There is no point in speculating as yet about the mechanism of this inhibition in the tentacles. Until we know more about the possible relationships between chemoreception, nematocyst discharge and nervous conduction, we cannot do more than describe the phenomena.

General inhibition during swimming

Most investigators who have studied the swimming behaviour of *Stomphia* have observed that during and for some time after swimming *Stomphia* is quite insensitive to stimulation. It may be handled and prodded without any of the usual withdrawal movements. During pauses in the swimming activity, or after the swimming activity comes to an end, the anemone usually lies on one side and is greatly distended. At this time it is easily carried away by the slightest current in the water. It shows no sign of movement or of the changes in shape which most anemones are making all the time. The tentacles are extended and quite immobile. It seemed desirable to study the nematocyst discharge of the tentacles to food and to *Dermasterias* in the various stages of the swimming response. In particular it seemed important to find out if the nematocyst discharge is inhibited in the same way as the response to general stimulation, and if so, to find out when the animal becomes insensitive and when it becomes responsive again.

After the usual controls single tentacles of ten experimental animals were touched with pipe cleaners rubbed on *Dermasterias* to evoke a swimming response. As soon as possible afterwards, usually within a few seconds, pipe cleaners dipped in the *Pecten* extract were brought into contact with 10 tentacles around the margin. This gave a score of the numbers of tentacles sticking to the pipe cleaner as an indication of the intensity of nematocyst discharge. The information from these tests is difficult to summarize in tabular form. We shall present, therefore, a general statement of the main findings and provide the data in full for our animal 6 only (Table 3). Three general observations were made.

(1) Almost as soon as *Stomphia* detaches its base from the surface to which it is attached, its tentacles become unresponsive to pipe cleaners dipped in the *Pecten* extract. This happens very suddenly; detachment seems to be the critical factor. In some cases when the swimming response is incomplete, it is possible to score an animal before detachment occurs, during the pre-swimming phase of the response. As long as the pedal disk remains attached, the tentacles are not unresponsive; they continue to stick to the pipe cleaners which have been dipped in the *Pecten* extract. Animal 6 in Table 3 provides an example of this sudden falling off in the nematocyst discharge to food precisely when the pedal disk becomes free. The suddenness of this transformation is a very important indication that the rise in the threshold of the nematocyst discharge is mediated via nerves and not by some diffuse chemical influence.

(2) The duration of the completely unresponsive condition of the tentacles was variable; it ranged from 5 to over 30 min. in different animals. Recovery once begun was fairly rapid. In our tests with 10 tentacles, the numbers of tentacles sticking to the pipe cleaners carrying the *Pecten* extract rose fairly quickly until all the tests gave positive results. The times taken for complete recovery of sensitivity ranged from about 20 to 60 min. (cf. animal 6 in Table 3).

Table 3. *Record of sequential tests of nematocyst discharge of tentacles of* Stomphia coccinea (*animal no.* 6)

10 tentacles touched with pipe cleaners (clean, dipped in *Pecten* extract, or rubbed on *Dermasterias*) to provide data on nos. of tentacles sticking (' + ') or not sticking (' − ') before, during and after the swimming response. Arrows show changes from low to high threshold and vice versa.

Test	Material on pipe-cleaner	Time after *Dermasterias*	Nematocyst discharges +	−	Behaviour and conditions of *Stomphia*
1	Clean	Control	0	10	Firmly settled on tile
2	*Pecten* extract	Control	9	1	Nematocyst discharge only
3	*Dermasterias* rubbing	0	1	.	Single contact on tentacle. *Stomphia* closed then opening rapidly
4	*Pecten* extract	5–11 sec.	10 ↘	0	*Stomphia* opening up. *Pedal disk still attached*
5	*Pecten* extract	15–23 sec.	0 ↙	10	*Stomphia* detached at 13 sec. Quiescent
6	*Pecten* extract	35–45 sec.	0	10	Intermittent swimming movements
7	*Pecten* extract	21 min.	0	10	Swimming ceased about 4 min. Position horizontal
8	*Pecten* extract	32 min.	0	10	*Stomphia* placed upright on tile. *Pedal disk not adhering*
9	*Pecten* extract	40 min.	7 ↘	3	Pedal disk expanded and *adhering to tile*
10	*Pecten* extract	44 min.	10	0	Pedal disk firmly attached to tile

(3) The return of responsiveness in the tentacles can be related to the first signs of reattachment of the basal disk. After swimming, *Stomphia* remains horizontal for a time, and during this period the basal disk shows no tendency to stick to the floor of the tank or to any objects lying in it. Quite suddenly, however, the basal disk becomes adhesive and the animal begins to attach itself to any available surface (Robson, 1961 *a*). Our records suggest that the recovery of sensitivity coincides with the appearance of the adhesive condition on the pedal disk (cf. Table 3).

The responses of *Stomphia* to other stimuli during the period of general inhibition were not studied in detail. We noted in passing whether the anemone's tentacles adhered to the fingers during swimming or afterwards. By this test the tentacles were 'not sticky' 19 times and 'sticky' 6 times. Evidently the inhibition of nematocyst discharge, which shows up so clearly in the standardized tests with individual tentacles, is not complete when the stimulus is massive and continuous. This suggests that the inhibition should be regarded not as an absolute block but as a condition in which the threshold for nematocyst discharge is very high.

The response of *Stomphia* to *Dermasterias* during and after swimming showed a similar situation. The tentacles were mostly unresponsive to pipe cleaners rubbed on *Dermasterias*, but when whole starfish were brushed over the tentacular crown, the results were inconsistent. Sometimes the tentacles stuck to the starfish, and sometimes

when this happened, swimming was resumed. On other occasions there was no response. This also looks like a threshold effect rather than an absolute inhibition.

When *Stomphia* is insensitive to handling after swimming it still gives the normal retraction response to electrical stimuli. This means that in the state of general inhibition during swimming, the ability of the nerve net to conduct impulses is not impaired. The inhibition, therefore, is apparently confined to the receptors, and is probably best regarded as a consequence of a general rise of the threshold of excitation of the receptors.

DISCUSSION

Davenport *et al.* (1961) and Ross & Sutton (1961) studied the responses of *Calliactis parasitica* to shells used by their hermit-crab partners. They found that the tendency of *Calliactis* tentacles to adhere to these shells was due to a discharge of nematocysts produced by a chemical shell-factor in the shell and in its periostracum. They also showed that this nematocyst discharge occurred about ten times as frequently (measured by counting numbers of single tentacles sticking to shells) in *Calliactis* not attached to shells as it does in *Calliactis* already settled on shells. They concluded tha information from the pedal disk controlled in some way the threshold of a nematocyst discharge evoked by contact with a shell.

In *Stomphia* also it now appears that information from the pedal disk determines whether the threshold for a nematocyst discharge to food is high or low. But compared with *Calliactis*, the relationship is reversed. In *Stomphia*, the threshold for nematocyst discharge is higher when the pedal disk is unattached; in *Calliactis*, it is higher when the pedal disk is settled on a shell. This is a good example of the flexible relationships between ends and means that are a feature of physiological adaptations. Yet the conclusion emerging from these studies on *Stomphia*, as on *Calliactis*, is that certain nematocysts of the tentacles are influenced by, and may themselves influence, neuromuscular processes going on elsewhere in these animals. Clearly the commonly held idea that nematocysts are strictly independent effectors is no longer a reliable generalization.

SUMMARY

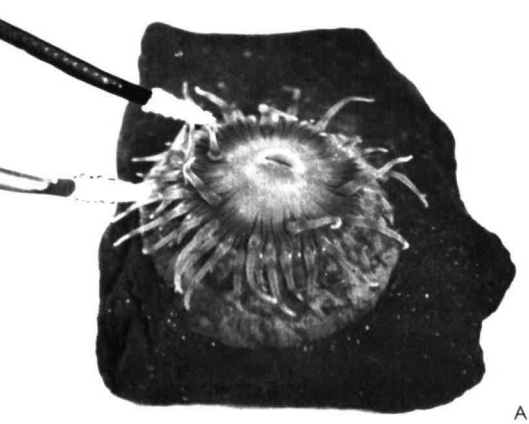
1. The discharge of tentacular nematocysts in response to food was studied in *Stomphia coccinea* before and during swimming, and during the period of resettling.

2. The tendency of *Stomphia*'s nematocysts to discharge on contact with food virtually disappeared during the swimming response. The disappearance of the nematocyst response coincided with the release of the pedal disk; its reappearance coincided with the re-attachment of the pedal disk.

3. Objects rubbed on the aboral surface of *Dermasterias* can cause swimming if brought into contact with a single tentacle of *Stomphia*.

4. A general inhibition of the swimming response to objects rubbed on *Dermasterias* was set up by flooding the tentacular crown with a food extract. A local inhibition was set up when food was applied to a single tentacle just before the same tentacle was touched with material from *Dermasterias*.

5. The results are discussed in relation to the view that nematocysts function as independent effectors.



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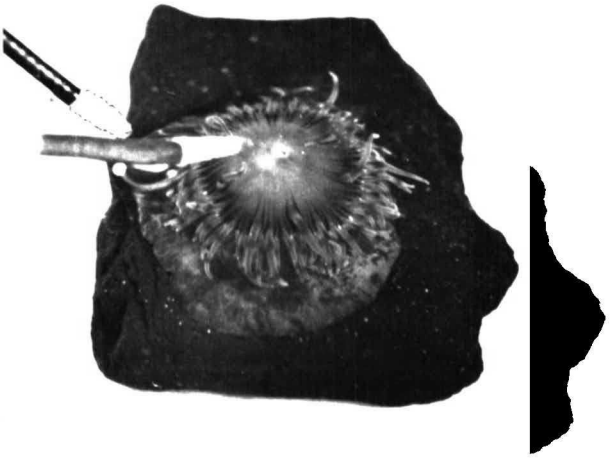

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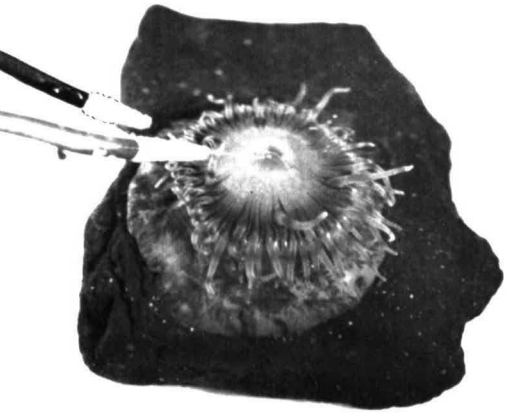

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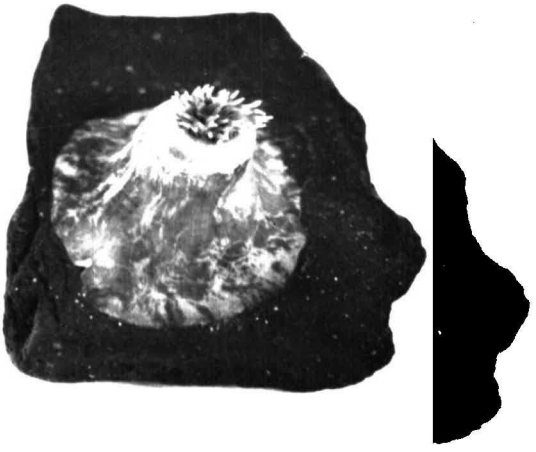

D

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REFERENCES

DAVENPORT, D., ROSS, D. M. & SUTTON, L. (1961). The remote control of nematocyst discharge in the attachment of *Calliactis parasitica* to shells of hermit crabs. *Vie et Milieu*, **12**, 197–209.

PANTIN, C. F. A. (1942). The excitation of nematocysts. *J. Exp. Biol.* **19**, 294–310.

ROBSON, E. A. (1961*a*). Some observations on the swimming behaviour of the anemone *Stomphia coccinea*. *J. Exp. Biol.* **38**, 343–63.

ROBSON, E. A. (1961*b*). The swimming response and its pacemaker system in the anemone *Stomphia coccinea*. *J. Exp. Biol.* **38**, 685–94.

ROSS, D. M. & SUTTON, L. (1961). The response of the sea anemone *Calliactis parasitica* to shells of the hermit crab *Pagurus bernhardus*. *Proc. Roy. Soc.* B, **155**, 266–81.

ROSS, D. M. & SUTTON, L. (1964). The swimming response of the sea anemone *Stomphia coccinea* to electrical stimulation. *J. Exp. Biol.* **41**, 735–49.

SUND, P. N. (1958). A study of the muscular anatomy and swimming behaviour of the sea anemone *Stomphia coccinea*. *Quart. J. Micr. Sci.* **99**, 401–20.

WARD, J. A. (1962). A further investigation of the swimming reaction of *Stomphia coccinea*. *Amer. Zool.* **2**, 567.

YENTSCH, C. S. & PIERCE, D. C. (1955). A 'swimming' anemone from Puget Sound. *Science*, **122**, 1231–3.

EXPLANATION OF PLATE

A. Single tentacle of *Stomphia coccinea* being touched by pipe cleaner dipped in *Pecten* extract.

B. 10–15 sec. after A, the same tentacle being touched by pipe cleaner rubbed on *Dermasterias*. No response occurred when *Pecten* extract preceded *Dermasterias*.

C. 5 mins. after A and B, another tentacle being touched by pipe cleaner rubbed on *Dermasterias*; pipe cleaner dipped in *Pecten* extract ready to be brought up to touch same tentacle immediately afterwards, i.e. reverse of experiment shown in A and B.

D. 5 sec. after C, *Stomphia* rising up after closure, the first stage in a swimming response which followed 15–20 sec. later. Full swimming response occurred when *Dermasterias* preceded *Pecten* extract.