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CHEMICAL RECOGNITION AND NEMATOCYTE EXCITATION IN A SEA ANEMONE

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SUMMARY

The response of nematocytes in the anemone *Stichodactyla haddoni* to contact with complex organic compounds varies according to the substance concerned and in most cases according to the level of accompanying mechanical stimulation. Compounds with a proteinaceous moiety differ in their capacity to excite nematocytes, but usually tend to induce a stronger response than polysaccharides or lipids. Nematocyst discharge against foreign animals appears to be the result of a sophisticated cellular recognition process in which the nematocytes, and/or cells closely associated with them, respond to physical contact with a surface of appropriate chemical composition.

INTRODUCTION

Nematocytes are unique stinging cells found in large numbers in cnidarians; each one contains an organelle known as a nematocyst which discharges explosively upon contact with a suitable substrate. The nature of organic substances that cause nematocyst discharge under natural conditions has received comparatively little attention since the research of Pantin (1942) on the constituents of food substances which excite the anemone *Anemonia sulcata*. Much work has been concentrated on the importance of substances such as glutathione in exciting cnidarian feeding receptors (Lenhoff, 1974), and this has tended to obscure the fact that little is known concerning the nature of compounds which excite the receptors associated with nematocytes. Most studies that have been carried out on nematocyst discharge have involved experimental manipulation of the environment (e.g. changes in ionic concentration; see review by Mariscal, 1974), and it is unclear how relevant the results obtained are to nematocyte excitation in the wild.

The present series of experiments was designed to determine which of the major categories of complex organic substances present on the surface of foreign animals would be most likely to elicit nematocyst discharge in the sea anemone *Stichodactyla haddoni* (the latter species was chosen as an experimental subject because its stinging response was particularly strong and readily quantifiable). This was carried out by presenting *S. haddoni* with glass rods coated in a variety of purified samples of proteins, glycoproteins, polysaccharides and lipids, and subsequently recording the animal's responses. As a comparison, a limited number of compounds was also offered to the anemone *Gyrostoma hertwigi*.

METHODS

Specimens of *Stichodactyla* (formerly *Stoichactis*) *haddoni* (Saville-Kent) (approx. 40 cm diameter) and *Gyrostoma hertwigi* Kwietniewski (approx. 15 cm diameter) were obtained from Sri Lanka and maintained in 150 l aquaria containing artificial sea water (Tropic Marin Neu; specific gravity 1·025) at 27 °C; the aquaria were brightly illuminated for 12 h per day. Anemones were fed on fish and prawn flesh. A single individual of each species was used in the following experiments, great care being taken to ensure that it was in good health (see below); no food was given for 3 days prior to an experiment lest recent food intake alter the level of nematocyst discharge (cf. Smith, Oshida & Bode, 1974).

Soda glass rods, 4·6 mm diameter with rounded ends, were cleaned for 20–40 min in chromic acid, rinsed several times in tap water and then distilled water, and finally dried. After coating with the appropriate compound, each rod was immersed in sea water for 2–3 s and presented to the experimental anemone.

Three major categories of substances were examined: (1) proteins and glycoproteins, (ii) polysaccharides and (iii) lipids. Each category was tested on a different day, preliminary controls having been carried out over several days to check that the anemone's responses did not vary significantly with time. Within each category different substances were interspersed with each other in a variety of orders; this was to prevent any possible changes in anemone condition during the experiment unevenly affecting the response to different compounds.

In view of differences in the overall ability of each category of compounds to adhere to a glass rod in sea water, coating of the rods was performed in a distinct manner for each category: (i) Proteins and glycoproteins (α-casein (bovine), cytochrome *c* (horse), γ-globulin (bovine), β-lactoglobulin (bovine), lysozyme chloride (hen), submaxillary mucin (bovine), myoglobin (whale), ovalbumin (hen), pepsin (porcine), serum albumin (bovine), trypsin (bovine)). Each glass rod was dipped for 5 s in an aqueous solution (1 % w/v) of poly-L-lysine (in order to enhance subsequent protein adhesion to rod; cf. Mazia, Schatten & Sale, 1975), rinsed in distilled water, and allowed to dry; the rod was then immersed for 5 s in a 1 % (w/v) aqueous solution of the appropriate compound and immediately presented to the anemone (rod not permitted to dry). Glass rods coated only in polylysine were used as controls. (ii) Polysaccharides (agarose, chondroitin 4-sulphate (whale), chondroitin 6-sulphate (shark), dextran, dextran sulphate, glycogen (oyster), heparin (porcine), hyaluronic acid (human), pectin (apple), starch (soluble)). Each rod was dipped for 5 s in a concentrated aqueous solution of the appropriate compound and immediately presented to the anemone. The concentration of each substance was generally determined by the amount required to produce a viscous mucus-like liquid. The following concentrations were used: agarose (0·5 % w/v), chondroitin 4-sulphate (30 % w/v), chondroitin 6-sulphate (30 % w/v), dextran (60 % w/v), dextran sulphate (60 % w/v), glycogen (30 % w/v), heparin (42 % w/v), hyaluronic acid (1·9 % w/v), pectin (15 % w/v), starch (15 % w/v) In the cases of agarose, starch and pectin, the solutions were liquefied by heating before immersing the rod. Clean glass rods, and rods coated with a viscous (2·5 % w/v) solution of submaxillary mucin, were used as controls. (iii) Lipids (cholesterol, cholesterol palmitate, lysolecithin (hen), oleic acid, palmitic acid, phosphatidyl choline,

phosphatidyl inositol (soya), phosphatidyl serine (bovine), squalene, triolein). Each rod was dipped for 5 s in a 0·1 % (w/v) solution of the appropriate compound in chloroform, allowed to dry, and then presented to the anemone. Controls used were as for polysaccharides.

In the case of *S. haddoni*, two methods of presentation were used. In the first method (termed touch method), the outer tentacles of the anemone were very gently touched with the rod; the rod was held still for 15 s, and then slowly moved and rotated among the tentacles for an additional 15 s. The second method (termed strike method) was similar to the first, except that initial contact was made by striking the rod against the anemone at a velocity of approximately 30–40 cm/s.

The reaction of *S. haddoni* was graded as either 0, 1 or 2, depending upon the number of tentacles adhering to the rod. [Tentacular adhesion in *S. haddoni* is directly related to nematocyst discharge: examination using a x100 NA 1·30 oil immersion objective with phase contrast of the traces remaining on objects to which tentacles had adhered revealed the presence in all cases of very large numbers of discharged nematocysts. The latter were tentatively identified using the key in Mariscal (1974) as isorhizas, most of which appeared to be basitrichous although a few may have been atrichous or holotrichous.] In the case of reaction type 0, no tentacles were observed to adhere to the rod end (distal 2 cm) during the presentation, and the edge of the anemone's disc did not retract more than 2 cm; in the case of type 1, less than 10 (usually 1–5) tentacles were observed to adhere to the rod end, and the edge of the anemone's disc did not retract more than 2 cm; in the case of type 2, more than 10 (usually at least 30) tentacles adhered to the rod end, and the edge of the anemone's disc retracted more than 2 cm (often up to 10–15 cm). Although careful observation was sometimes necessary to distinguish between reactions of type 0 and type 1, type 2 was quite distinct. Fig. 1 shows rods that have been stained with Coomassie blue after presentation to *S. haddoni*: the rods which produced a type 0 or type 1 reaction are essentially clear, while those that produced a type 2 reaction are dark with discharged nematocysts. It is worth noting that the tentacles' ability to adhere to a glass rod seemed to be independent of the presence of organic substances on the rod tip. If a clean glass rod was placed against the tentacles no adhesion occurred; however, a 70 V pulse for 10 ms in the close vicinity of the rod tip caused a number of tentacles to adhere strongly to the glass.

Differences in the morphology of *G. hertwigi's* tentacles prevented their reactions being measured in the same fashion as those of *S. haddoni*. For *G. hertwigi*, each rod was very gently touched for 5 s against the tip of one tentacle; a record was made of whether or not the tentacle adhered to the rod. Rods presented to *G. hertwigi* were prepared in an identical manner to those used on *S. haddoni*. In the case of bovine submaxillary mucin, only the preparation method involving immersing a clean rod in a 2·5 % w/v solution was used for presentation to *G. hertwigi*.

Tropical sea anemones kept under poor aquarium conditions cease to feed, and gradually shrink, often over a period of several months, until finally they die. It is characteristic of such anemones that the tentacles become progressively shorter, and fail to adhere upon contact with prey (cf. Mariscal, 1971).

The adhesive force of *Stichodactyla haddoni* was measured by attaching 16 × 16 mm coverslips coated with congealed 60 % (w/v) gelatine solution to a spring balance.

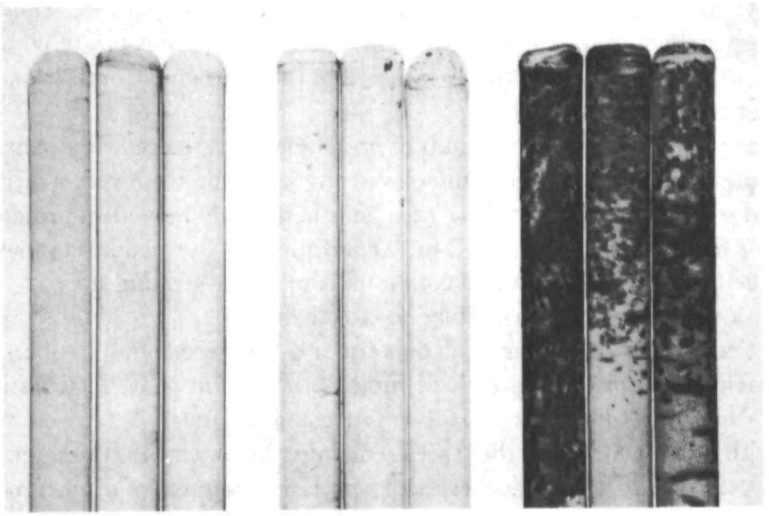

Fig. 1. Glass rods (4·6 mm in diameter) that have been stained with Coomassie blue after presentation to *Stichodactyla haddoni*: the three rods on the left induced a type 0 response, the centre three a type 1 response, and the right hand three a type 2 response (see Methods for explanation of response types).

Table 1. *The number of tentacles discharging onto gelatine-coated coverslips* (16 × 16 mm), *and the adhesive force per tentacle, in two specimens of* Stichodactyla haddoni

Test animal	Number of tentacle traces per coverslip		Adhesive force per tentacle (g)		
	Range	Mean	Range	Mean	*n*
Stichodactyla haddoni (22 cm diameter; healthy)	33–85	59·3	0·63–1·14	0·86	10
Stichodactyla haddoni (21 cm diameter; unhealthy)	0–7	2·3	0	0	3

Adhesive force of < 0·3 g recorded as 0.

Each coverslip was allowed to contact the anemone's outer tentacles (i.e. tentacles < 2 cm from disc edge) for ½–1 s before the animal's adhesion was measured; care was taken to ensure that only the lower surface of the coverslip came into contact with the anemone. The adhesive force was defined as that force required to make the anemone relinquish the coverslip. The number of discrete areas of nematocyst discharge visible on the gelatine at × 12 magnification after staining with 0·5 % methylene blue was counted and divided into the total adhesive force for the coverslip, to give adhesive force per tentacle. Table 1 compares the stinging abilities of a normal anemone (22 cm diameter) with those of an unhealthy specimen (21 cm diameter). Tentacular adhesion was pronounced in the former, while it was virtually absent in the latter.

It is clear that loss of condition in an experimental anemone can easily result in misleading data, and great care was taken to ensure that anemones used were in good health. Aquarium specimens were compared with descriptions and photographs of the same species made under natural conditions, and the anemones' reactions to prey

Table 2. *Response of* S. haddoni *to proteins and glycoproteins. Responses graded as* 0 (*none*), 1 (*poor*), *or* 2 (*strong*); *rods presented either by touch method or by strike method* (*for precise definitions of grades of response and of rod presentation techniques, see Methods*)

	Touch method			Strike method			
Compound	0	1	2	0	1	2	*n*
Glass rod + polylysine (control)	20	–	–	19	1	–	40
Cytochrome *c*	4	1	–	3	1	1	10
Pepsin	5	–	–	–	2	3	10
Trypsin	4	–	1	2	1	2	10
Lysozyme chloride	4	–	1	1	–	4	10
Ovalbumin	4	–	1	1	–	4	10
Myoglobin	2	2	1	–	–	5	10
Serum albumin	1	–	4	–	–	5	10
γ-globulin	–	1	4	–	–	5	10
Submaxillary mucin	–	1	4	–	–	5	10
β-lactoglobulin	–	–	5	–	–	5	10
α-casein	–	–	5	–	–	5	10

Vertical lines indicate subsets of responses that are not significantly different ($P > 0.05$).

Table 3. *Response of* S. haddoni *to polysaccharides. Responses graded as* 0 (*none*), 1 (*poor*), *or* 2 (*strong*); *rods presented either by touch method or by strike method* (*for precise definitions of grades of response and of rod presentation techniques, see Methods*)

	Touch method			Strike method			
Compound	0	1	2	0	1	2	*n*
Glass rod (control)	5	–	–	5	–	–	10
Agarose	5	–	–	5	–	–	10
Chondroitin 4-sulphate	5	–	–	5	–	–	10
Chondroitin 6-sulphate	5	–	–	5	–	–	10
Dextran	5	–	–	5	–	–	10
Dextran sulphate	5	–	–	5	–	–	10
Heparin	5	–	–	5	–	–	10
Pectin	5	–	–	5	–	–	10
Starch	5	–	–	4	1	–	10
Glycogen	4	1	–	3	2	–	10
Hyaluronic acid	–	3	2	–	2	3	10
Submaxillary mucin (control)	–	–	5	–	–	5	10

Vertical lines indicate subsets of responses that are not significantly different ($P > 0.05$).

substances were tested. In the case of *S. haddoni*, an animal was considered healthy if it was fully inflated (individuals occasionally contracted below the sand for a few hours) if its tentacles were elongate (between 3 and 8 mm long for a 40 cm diameter individual), if it responded rapidly and positively to contact with food (e.g. pieces of prawn flesh), and if it adhered densely to a glass rod coated in human saliva.

For Tables 2, 3, 4 and 6, pairwise comparisons amongst the treatments were carried out by applying the 'exact' test for a contingency table (Freeman & Halton, 1951).

Table 4. *Response of* S. haddoni *to lipids. Responses graded as* 0 (*none*), 1 (*poor*), 2 (*strong*); *rods presented either by touch method or by strike method (for precise definitions of grades of response and of rod presentation techniques, see Methods)*

	Touch method			Strike method			
Compound	0	1	2	0	1	2	*n*
Glass rod (control)	5	–	–	5	–	–	10
Cholesterol	5	–	–	5	–	–	10
Cholesterol palmitate	5	–	–	5	–	–	10
Oleic acid	5	–	–	5	–	–	10
Phosphatidyl choline	5	–	–	5	–	–	10
Lysolecithin	5	–	–	4	1	–	10
Palmitic acid	5	–	–	4	1	–	10
Squalene	5	–	–	4	1	–	10
Phosphatidyl inositol	5	–	–	3	1	1	10
Triolein	5	–	–	2	2	1	10
Phosphatidyl serine	3	1	1	1	2	2	10
Submaxillary mucin (control)	–	–	5	–	–	5	10

Vertical lines indicate subsets of responses that are not significantly different ($P > 0{\cdot}05$).

RESULTS

The reactions of *Stichodactyla haddoni* to a selection of proteins and glycoproteins are shown in Table 2. There were clear differences in the levels of response to the various substances. Using the touch method of presentation, ovalbumin, lysozyme chloride, trypsin, pepsin and cytochrome *c* all failed to induce a response that was significantly greater than that of the glass rod control; myoglobin induced an intermediate response, while α-casein, β-lactoglobulin, submaxillary mucin, γ-globulin and serum albumin produced strong reactions. Using the strike method of presentation, all substances except cytochrome *c* produced a reaction that was significantly greater than that of the control.

Table 3 shows the anemone's reactions to polysaccharides. Only hyaluronic acid managed to cause a reaction that was significantly different from that of the glass rod control.

Table 4 shows the responses of *S. haddoni* to lipids. The only test substance to induce a response that was significantly greater than that of the glass rod control was phosphatidyl serine (when applied by the strike method).

Given that, at the moment of contact with the anemone, the amount of each compound present on the rod tip could not be accurately determined, the above results need to be interpreted with care, especially when comparing different categories of compound. Nevertheless, it is clear that the polysaccharides, which were usually present in sufficient quantity to be clearly visible on the rod tip after immersion in sea water, failed to elicit a type 2 (i.e. strong) reaction in all but the case of hyaluronic acid. In contrast the proteins and glycoproteins, which were probably present on the rod in most cases as a layer only a few molecules thick, were all able to produce type 2 reactions to a varying extent, although there appeared to be marked differences in overall reactivity. Lipids, which were also present on the rod in rather low quantities, were generally unreactive, with only 3 out of 10 substances being capable of producing a type 2 reaction on any occasion. The percentage distributions of the different grades

Table 5. *Percentage distribution of* S. haddoni *responses. For each presentation method, the percentages of all the rods coated with a given category of compounds that produced type* 0 *(none), type* 1 *(poor) and type* 2 *(strong) reaction are shown (for precise definitions of grades of response and of rod presentation techniques, see Methods)*

	Touch method (%)			Strike method (%)		
Category of compound	0	1	2	0	1	2
Protein and glycoprotein	44	7	49	13	7	80
Polysaccharide	88	8	4	84	10	6
Lipid	96	2	2	66	16	8

Table 6. *Response of* G. hertwigi *to various compounds, principally polysaccharides. Adhesion of a tentacle is shown as* +, *non adhesion as* −

	Adhesion		
Compound	−	+	*n*
Agarose	15	−	15
Chondroitin 4-sulphate	15	−	15
Chondroitin 6-sulphate	15	−	15
Dextran sulphate	15	−	15
Heparin	15	−	15
Glass rod (control)	14	1	15
Pectin	14	1	15
Hyaluronic acid	10	5	15
Starch	8	7	15
Glycogen	2	13	15
Polylysine	1	14	15
Submaxillary mucin	1	14	15

Vertical lines indicate subsets of responses that are not significantly different ($P > 0.05$).

of *S. haddoni* response in each overall category, for both touch method and strike method respectively, are shown in Table 5.

If one compares the anemone's response using the touch and strike methods of presentation, it becomes apparent that for 14 substances there were no differences in response, while for the 17 other substances there was an increase in the overall response using the latter method. Thus the strike method, which involved increased mechanical stimulation, never caused a decrease in reaction, and in the majority of cases increased the reaction.

The reactions of *G. hertwigi* to a limited number of substances are shown in Table 6. The presentation method used for *G. hertwigi* (see Methods) was in many ways analogous to the touch method of presentation for *S. haddoni*; the reactions of *G. hertwigi* shown in Table 6 should be compared to *S. haddoni's* reactions to the same compounds in Tables 2 and 3. For *G. hertwigi*, it will be seen that agarose, chondroitin 4-sulphate, chondroitin 6-sulphate, dextran sulphate, heparin, pectin, and hyaluronic acid did not produce a response significantly different from that of the glass rod control; starch produced a moderate response, while glycogen, polylysine and submaxillary mucin produced a strong reaction. Overall the responses of *G. hertwigi* seemed to be rather similar to those of *S. haddoni; G. hertwigi* did, however,

show a greater response to starch and especially to glycogen and polylysine than *S. haddoni*.

DISCUSSION

The above experiments demonstrate that chemicals present on the surface of an object contacting *Stichodactyla haddoni* are important in determining whether nematocyst discharge occurs. The anemone was clearly able to distinguish between different organic compounds, and within each major category of compounds investigated there were frequently quite marked differences in the extent of the animal's response to each substance. Overall, proteins and glycoproteins produced the strongest nematocyst discharge, although it should be noted that the response to certain proteins (e.g. cytochrome *c*, pepsin and trypsin) was relatively weak, especially when using the touch method of presentation. The polysaccharides examined were, with one exception, rather unstimulatory, as were also the majority of lipids. Of the 15 substances capable of producing one or more instances of a strong (i.e. type 2) response, 11 contained proteinaceous moieties. Pantin's (1942) work on the anemone *Anemonia sulcata* indicated that the nematocytes were sensitized not by proteins themselves but rather by lipoid substances strongly adsorbed onto proteins. This seems different from the situation in *S. haddoni*, in which certain purified samples of protein (as well as some glycoproteins, lipids and polysaccharides) were found to induce strong nematocyst discharge.

Substances could be classified into two groups in terms of the response that they engendered from *S. haddoni*. Those in the first group induced a response that was not altered by differences in the level of accompanying mechanical stimulation; this group thus contained compounds that were either highly stimulatory (e.g. submaxillary mucin) or else quite unstimulatory (e.g. chondroitin sulphate). The second and largest group consisted of compounds whose ability to incite nematocyst discharge appeared to be increased if accompanied by strong mechanical stimulation (cf. Pantin, 1942; Conklin & Mariscal, 1976). Levels of mechanical stimulation used in the above experiments were of the order of magnitude that might be expected under natural conditions; it does of course remain possible that even the most inert substances might provoke discharge if accompanied by extreme mechanical stimuli.

Comparison of the responses of *Stichodactyla haddoni* and *Gyrostoma hertwigi* indicated a marked similarity between the two species, although *G. hertwigi* showed increased sensitivity to certain compounds. Differences in the sensitivity of anemones to various compounds may be an important factor in explaining results such as those of Schlichter (1968), where in some cases a symbiotic clownfish (*Amphiprion*) living unharmed in one species of anemone was unable to enter directly into another anemone species without being stung.

Nematocyst discharge against foreign animals may be regarded as the result of a cellular recognition process in which the nematocytes, and/or cells closely associated with them (Mariscal & Bigger, 1976), respond to physical contact with a surface of appropriate chemical composition. The receptors associated with nematocyst discharge can be sensitive to comparatively subtle chemical differences, as for example the anemone *Anthopleura elegantissima* where intra- and extra-clonal conspecifics induce different responses (Francis, 1973). Although nematocytes were previously

thought to be independent effectors, it is now known that the extent of nematocyst discharge can vary according to the physiological condition of the host animal (see Conklin & Mariscal, 1976): for example Smith *et al.* (1974) have indicated that in *Hydra attenuata* the discharge of nematocytes used in prey capture (stenoteles and desmonenes) may be inhibited by high concentrations of metabolites arising from overfeeding. Various authors (e.g. Schlichter, 1972; Wright, 1973) have suggested that cnidarians might possess specific nematocyte inhibitors on their external surfaces to prevent them stinging themselves, but there is at present no clear evidence on which to base such an assertion. An alternative and perhaps more likely possibility is that those chemical groups to which nematocytes respond are absent from the external surfaces of the animal; the fact that the cnidarian does not sting itself can then be explained in terms of its nematocytes not receiving the appropriate stimuli rather than in terms of active nematocyte inhibition. An interesting question which would seem to deserve further attention is how the functioning of nematocytes used against foreign animals compares with that of those used in locomotion (cf. Ewer, 1947).

In summary, the response of *Stichodactyla haddoni's* nematocytes to contact with complex organic substances of the kind that might occur on the surface of a foreign animal varied according to the substance concerned and in most cases according to the level of accompanying mechanical stimulation. Compounds with a proteinaceous moiety differed in their capacity to excite nematocytes, but usually tended to induce a stronger response than polysaccharides or lipids. No simple basis could be determined for the manner in which *S. haddoni* recognized the different compounds, and it seems likely that recognition processes associated with nematocyst discharge may be of a rather sophisticated nature.

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