

On Triggering and Control of Cnidocyst Discharge

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Ultrastructural and *in vivo* observations in several planktonic coelenterates show that the cnidocytes, always associated with a receptor pole (the cnidocil itself or an accessory sensory cell) may have no link with the nervous system, or may be associated with it.

On the basis of these observations we propose that the cnidocytes of physonect siphonophores can be placed in two categories of receptor-effectors both sensitive to stimuli received by the cnidocil. The cnidocytes of the first category, with defensive functions, localized on the pneumatophore, nectophores and bracts, have no link with the nervous system and are typical independent receptor-effectors. In contrast, those of the second category whose distribution on the fishing tentacles and gastrozooids, implies predatory functions, are connected with the nervous system which may modulate or control their thresholds of excitability. Thus, in one and the same animal, depending on their function, the cnidocytes may or may not be linked with the nervous system, a difficult and long debated question in most of the cnidarians.

INTRODUCTION

The cnidocyte is a cell which has an external apical receptor and an effector structure, the cnidocyst, which can suddenly evaginate its filament when appropriately stimulated (Figure 1).†

The existence of a receptor system and an effector system within one and the same cell has long classed cnidocytes as independant receptor-effectors (Wagner, 1905; Parker and Van Alstyne, 1932; Pantin, 1942; Ewer, 1947; Jones, 1947; Bullock and Horridge, 1965; Picken and Skaer, 1966). However, ultrastructural observations have called this interpretation in question. Lentz and Baarnett (1965), Jha and Mackie (1967), Slautterback (1967) have pointed

† Throughout, the whole cell is always designated by the term cnidocyte and the capsule by the term cnidocyst.

out the presence of numerous neurites in the vicinity of cnidocytes. Westfall (1969, 1970a, 1970b) and Westfall *et al.* (1971) observed synapses close to cnidocytes in *Hydra* and *Gonionemus*. From another point of view, Glumac (1953), Burnett *et al.* (1960), Bouchet (1961), Mariscal (1973), Smith *et al.* (1974) showed that cnidocyst discharge is correlated with the nutritional condition of the animal. Finally, Conklin and Mariscal (1976) pointed out an increase in the rate of evagination of tentacle cnidocysts in *Anemonia sargassensis* after stimulation of the gastric column.

In this paper, we report ultrastructural and "in vivo" observations bearing on the question of whether the nervous system is necessarily involved in cnidocyst discharge.

MATERIAL AND METHODS

We have worked on planktonic coelenterates, mainly on the siphonophores *Muggiae kochi*, *Apolemia uvaria*, *Cordalgama cordiformis*, the chondrophore *Porpita porpita*. Some observations were made on the ctenophore *Euchlora rubra* and on the scyphomedusa *Nausithoe punctata*.

The different types of cnidocysts are identified according to Weill (1934) and Mariscal (1974).

Living material was examined with Nomarski interference contrast optics. For electron microscopy, material was fixed in 3% glutaraldehyde in cacodylate buffered sodium chloride solution of sea water osmolarity (pH 7.4) and postfixed in 1% osmium tetroide in sea water. The specimens were then dehydrated and embedded in Spurr resin.

ULTRASTRUCTURAL ORGANISATION OF CNIDOCILIAR APPARATUS

All the cnidocytes studied, except those of *Euchlora*, have a cnidocil. In cross section, together with the nine typical doublets there are additional tubules varying in number from a few up to 100 (Figure 2-4). At the base of the cnidocil a collarette is formed which is either continuous or consist of a series of villi thus forming a corolla.

The collarette and the cnidocil, separated by a regular space, form a structure comparable to the receptor pole of cnidarian sensory cells as defined by Horridge (1969).

As in the case of sensory cells, septate desmosomes are found between the collarette and the adjacent epithelial cells (Figure 5). Furthermore, in the tentilla of siphonophores, we have observed direct contacts between cnidocil and epithelial cells. These contacts, which have not been observed previously, are similar to classic septate desmosomes (Figure 5).

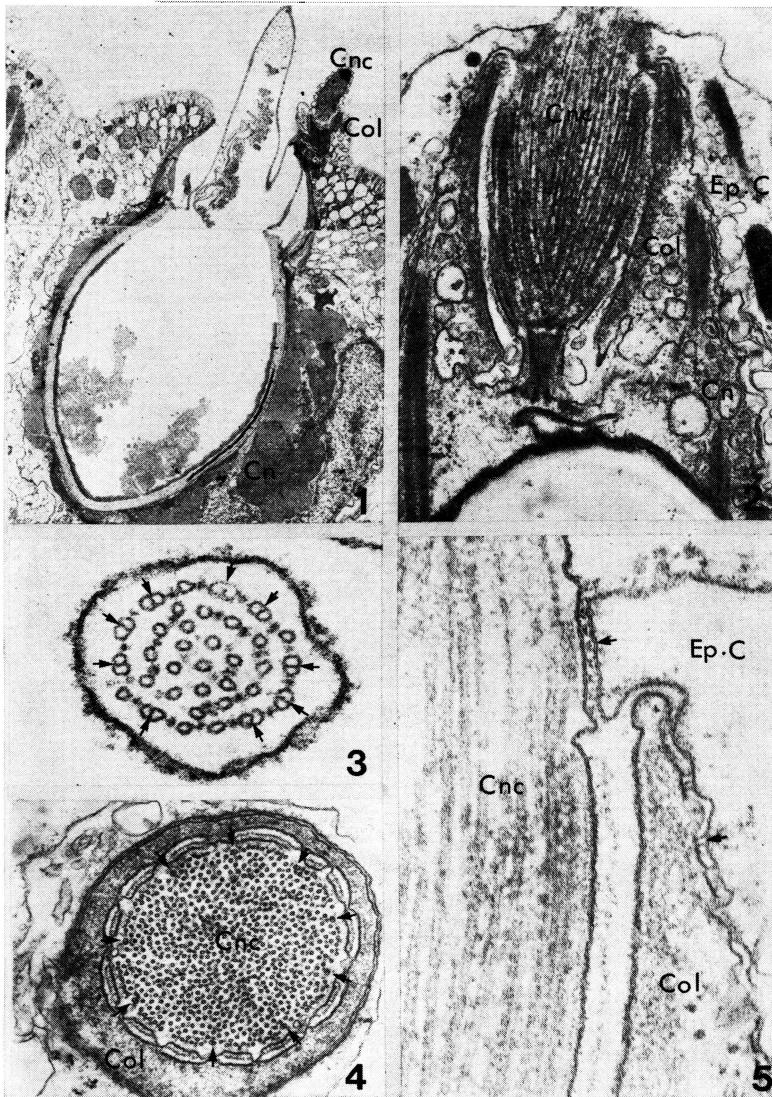


FIGURE 1 *Porpita porpita* (Chondrophora): stenotele during evagination. ($\times 4000$).

FIGURE 2 *Muggiaeae kochi* (Siphonophora calycophorae): longitudinal section of a desmoneme cnidocil ($\times 30,000$).

FIGURE 3 *Muggiaeae kochi*: cross section of an anisorhiza cnidocil ($\times 10,000$).

FIGURE 4 *Muggiaeae kochi*: cross section of desmoneme cnidocil ($\times 40,000$) showing the collarette around the cnidocil.

FIGURE 5 *Muggiaeae kochi*: desmoneme, detail of junctions with the adjacent epithelia cell.

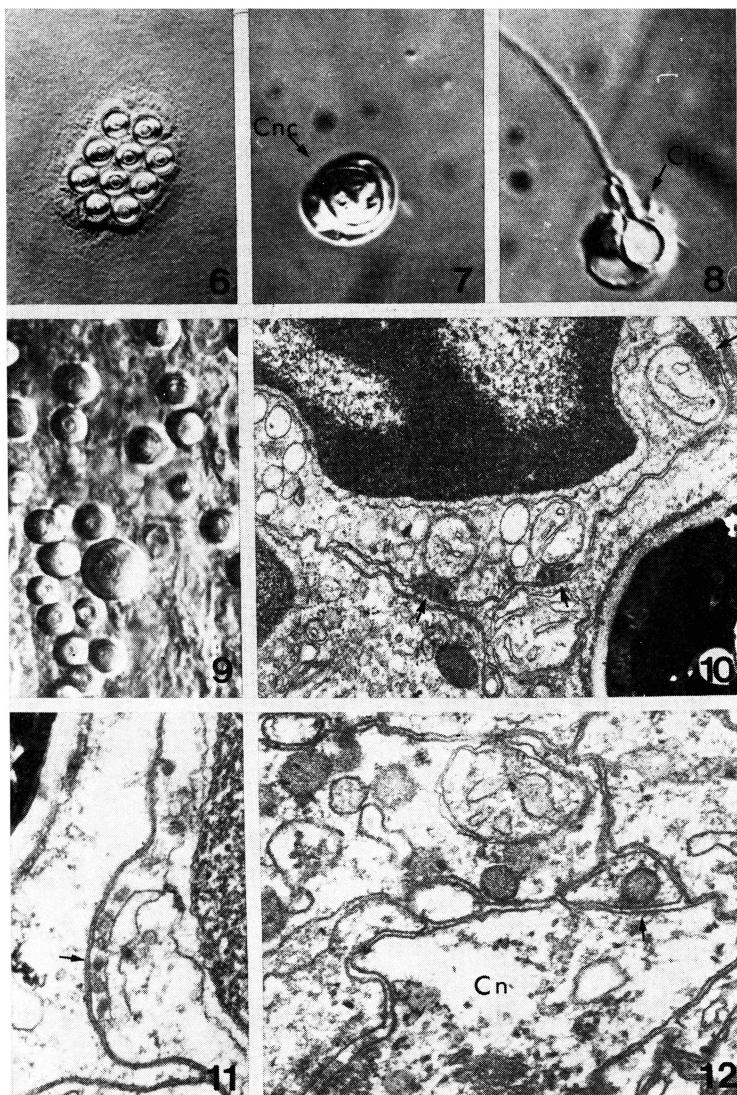


FIGURE 6 *Apolemia uvaria*: (Siphonophora physonectae): groups of isorhizas in the epithelium of the bract ($\times 500$).

FIGURE 7 *Nausithoe punctata* (Scyphomedusae): microbasic eurytele enveloped by its cnidocyte in the egg coat ($\times 5000$).

FIGURE 8 *Nausithoe punctata*: evaginated microbasic eurytele in the egg coat.

FIGURE 9 *Euchlora rubra* (Ctenophora): microisorhizas and macroisorhizas ($\times 1400$).

FIGURE 10 *Euchlora rubra*: neuro-effector synapses between a sensory cell and an endodermal cell fragment containing an exogenic cnidocyste ($\times 15,000$).

FIGURE 11 *Euchlora rubra*: neuro-effector synapses between a sensory cell and an endodermal cell fragment containing an exogenic cnidocyste ($\times 30,000$).

FIGURE 12 *Apolemia uvaria*: neuro-effector synapses between neurites and the podocyte of a cnidocyte ($\times 60,000$).

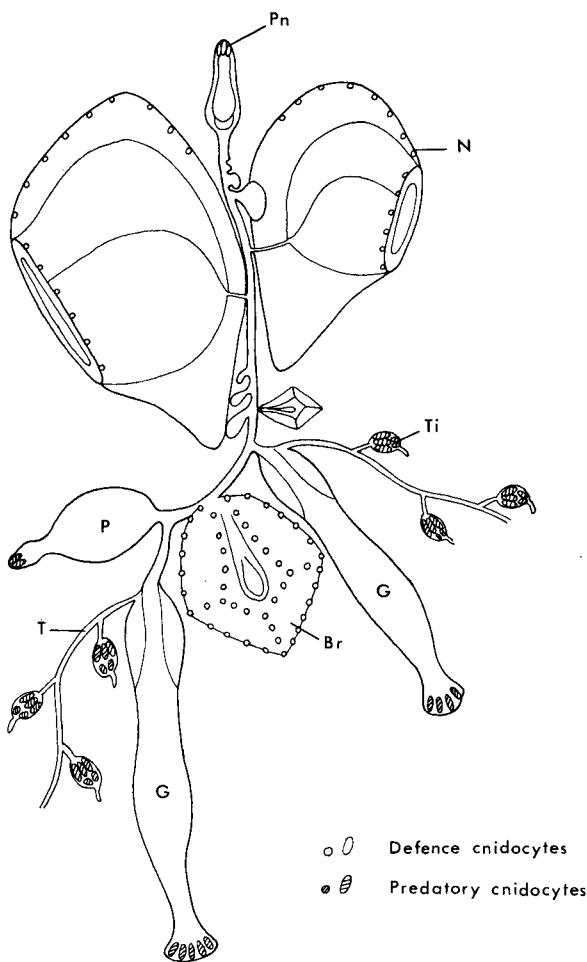


FIGURE 13 *Cordagalma cordiformis* (Siphonophora physonectae): schematic drawing of the distribution of predatory and defence cnidocytes in a young colony (1 cm long).

Br.	bract	Col.	collarette	N.	nectophore
Ep.c.	epithelial cell	P.	palpon	Pn.	pneumatophore
Cn.	cnidocyte	T.	tentacle	Ti.	tentilla
Cnc.	cnidocil	G.	gastrozoid		

CONTROL OF TRIGGERING IN CNIDOCYST DISCHARGE

We deal with this question by examining special cases which pose the problem in simplified terms.

1) Is the nervous system essential for the normal triggering of evagination?

a) Isorhizas in the bracts of *Apolemia uvaria*.

Apolemia uvaria is a big physonect siphonophore (up to 40 meters long) whose cormidia bears numerous hemispherical bracts. Each bract is formed by an ectodermal layer, and an endodermal canal, separated by a thick mesogleal layer. The ectoderm is totally devoid of nervous structures, which have never been seen either with the optical or electron microscope. It is dotted with groups of five to ten isorhizas (Figure 6). They are abundant in the young bracts, their number decreases as the bract is older and they are often absent in the old bracts which suggests that they are functional. In the laboratory, it is possible to obtain their triggering by mechanical stimulation or by adding chloral hydrate solution (Totton, 1974).

This example illustrates a case of cnidocytes evaginating without any possible direct link with the nervous system. However it is possible to suggest an indirect control via aneural conduction. Indeed it is known that the epithelia of siphonophores are excitable and capable of transmitting action potentials independently of the nervous system (Mackie, 1965).

b) Stenoteles of *Nausithoe punctata* eggs.

When they have been laid, the eggs of this medusa are enveloped by a thick gelatinous coat. On the surface of this coat there are scattered small isolated cnidocytes with cnidocils (Figure 7). It is possible, by mechanical stimulation or by putting the egg in contact with predators, to obtain evagination of these capsules which are microbasic euryteles (Figure 8).

This case is an example of evagination occurring without any possible intervention, not only of the nervous system but also of aneural conducting systems. It illustrates perfectly the case of the cnidocyte as an independent effector.

2) Is the cnidocil indispensable for triggering of normal evagination?

The exact role of the cnidocil is difficult to study directly without very delicate mechanical stimulation. But the question may be approached indirectly in some animals such as eolidian molluscs or the ctenophore *Euchlora rubra*, which ingest cnidarians and retain their cnidocysts. It seems that only the capsule is integrated in the host tissues, whereas the cnidocyte and its cnidocil are digested.

We studied the case of *Euchlora rubra* with the TEM. In this ctenophore, in the place of the usual colloblasts there are two rows of functional cnidocysts (Figures 9, 10). We have shown (Carré and Carré, 1980) that these cnidocysts have an exogenous origin. They are effectively devoid of cnidocyte and cnidocil and are merely enveloped by a little cytoplasm and a membrane derived from the endodermic cell which phagocytosed the cnidocyst. The interesting fact is that this anucleate cell fragment associated with the cnidocyst is in synaptic connection with a sensory cell of the ctenophore (Figures 10, 11).

This example illustrates the requirement for a receptor to be associated with the capsule for its evagination. A similar situation presumably occurs in those molluscs which possess functional cnidocysts.

3) Does the nervous system intervene in the evagination of some cnidocysts?

Our observations on siphonophores and those of Westfall on *Hydra* and *Gonianemus*, show synapses between neurites and cnidocytes (Figure 12). These endings have obviously a functional significance confirmed by recent studies on cnidarian physiology which we shall consider in the discussion.

4) Can cnidocytes be connected or unconnected with the nervous system in the same cnidarian?

In physonect siphonophores such as *Apolemia* or *Cordagalma* (Figure 13) neurites and sometimes synapses occur close to the cnidocytes of the fishing filaments and gastrozooids (Figure 12). In contrast, the cnidocytes of the bracts, nectophores and pneumatophore are never connected with the nervous system. It is known that the bracts are devoid of nervous structures. In nectophores and pneumatophore the neurones are localized in special areas different from those where cnidocytes are found.

The first category of cnidocytes which may be linked with the nervous system, catches the prey. The distribution of the second category which is unconnected to the nervous system, implies a defensive function.

We must specify that all the cnidocysts in the cnidosacs of tentacles are not directly innervated. The sensory cells and neurites are present only at the base of each cnidosac, the major part being constituted by closely packed cnidocytes. Synapses can be observed only between sensory cells and the adjacent cnidocytes. It is probable that, beyond this system, an influx of aneural type is propagated from cnidocyte to cnidocyte as they all exploded simultaneously.

DISCUSSION AND CONCLUSIONS

The examples quoted above permit some preliminary conclusions. First the cnidocyte always requires an external receptor. If the cnidocil has disappeared (as in the case of *Euchlora isorhizas*) an accessory sensitive structure is

associated with the capsule. Secondly, our observations of the euryteles in the egg coat of *Nausithoe punctata* confirm that cnidocytes may be independent receptor-effectors. However, this does not rule out the involvement of the nervous system in other cases, as indicated by the existence of neuro-cnidocytic synapses.

We propose an interpretation based on a physonect siphonophore study which reconciles these partial conclusions. We suggest that triggering itself is always independent of the nervous system: the cnidocil receives external stimuli and, whenever a given stimulus exceeds the threshold of excitability the cell responds by evagination of its filament. The defence cnidocytes of the bracts, nectophores and pneumatophore unconnected with the nervous system, must have a fixed threshold and inevitably respond to any stimuli equal or superior to this threshold. The case of the predatory cnidocytes of the fishing tentacles and gastrozooids, possibly linked with the nervous system, seems more complex. In our view, their excitation threshold may be controlled and modulated by the nervous system in terms of the physiological conditions of the animal but the evagination process itself must be independent of the nervous system.

The interest of this example is to show that there is no contradiction as was previously supposed (see Mariscal, 1974 for review) between the notion of a receptor–effector and an eventual dependence on the nervous system. The conflicting accounts of previous authors may be explained by the coexistence in all the cnidarians, of two classes of cnidocytes, the one connected with the nervous system (such as predatory cnidocytes of siphonophore) and the others completely independent (such as defence cnidocytes of siphonophores). Therefore, in many cnidarians, the demonstration of this situation seems more difficult than in physonect siphonophores.

Bibliography

- Bouchet, C. (1961). Le contrôle de la décharge nématocystique chez l'Hydre. *C.R. Acad. Sc. T.* **252**, 327–328.
- Bullock, T. H. and Horridge, G. A. (1965). *Structure and Function in the Nervous Systems of Invertebrates*. Vol. I. Freeman, San Francisco, California, 798 pp.
- Burnett, A. L., Lentz, T. and Warren, M. (1960). The nematocyst of *Hydra* (Part I). The question of control of the nematocyst discharge reaction by fully fed hydra. *Ann. Soc. Roy. Zool. Belg.* **90**, 247–267.
- Carré, C. and Carré, D. (1980) Cah. Biol. Mar. Les nématocystes du Cténophore *Euchlora rubra* (Kölliker, 1852) (In press).
- Conklin, E. J. and Mariscal, R. N. (1976). Increase in nematocyst and spirocyst discharge in a sea anemone in response to mechanical stimulation. In: *Coelenterate Ecology and Behavior*, edited by G. O. Mackie. Plenum Press, New York, pp. 549–558 (pages of article referred to).
- Ewer, R. F. (1947). On the functions and mode of action of the nematocysts of *Hydra*. *Proc. Zool. Soc. London*, **117**, 365–376.
- Glumac, S. (1953). Contribution à la connaissance du fonctionnement des cellules à nématocystes chez l'Hydre d'eau douce. *Glasn. Mus. Zrpsk. Zeml (B)*, **5–6**, 503–511.

- Horridge, G. A. (1969). Statocysts of medusae and evolution of stereocilia. *Tissue and Cell*, **1**, 341–353.
- Jha, R. K. and Mackie, G. O. (1967). The recognition, distribution and ultrastructure of hydrozoan nerve elements. *J. Morphol.* **123**, 43–61.
- Jones, C. S. (1947). The control and discharge of nematocysts in *Hydra*. *J. Exp. Zool.* **105**, 25–60.
- Lentz, T. L. and Baarnett, R. J. (1965). Fine structure of the nervous system of *Hydra*. *Amer. Zool.* **5**, 341–356.
- Mackie, G. O. (1965). Conduction in the nerve-free epithelia of siphonophores. *Amer. Zool.* **5**, 439–453.
- Mariscal, R. N. (1973). The control of nematocyst discharge during feeding by sea anemones. *Publ. Seto Mar. Biol. Lab.* **20**, 695–702.
- Mariscal, R. N. (1974). Nematocysts. L. Muscatine and H. M. Lenhoff (Eds.). *Coelenterate Biology*. Academic Press, New York, pp. 129–178.
- Pantin, C. F. A. (1942). The excitation of nematocysts. *J. Exp. Biol.* **19**, 294–310.
- Parker, G. H. and Van Alstyne, M. A. (1932). The control and discharge of nematocysts, especially in *Metridium* and *Physalia*. *J. Exp. Zool.* **63**, 329–344.
- Picken, L. E. R. and Skaer, R. J. (1966). A review of researches on nematocysts. *Symp. Zool. Soc. London*, **16**, 19–50.
- Slauterback, D. B. (1967). The cnidoblast-musculoepithelial cell complex in the tentacles of *Hydra*. *Z. Zellforsch. Mikrosk. Anat.* **79**, 296–318.
- Smith, S., Oshida, J. and Bodes, H. (1974). Inhibition of nematocyst discharge in hydra fed to repletion. *Biol. Bull.* **147**, 186–202.
- Totton, A. K. (1974). A method for discharging nematocysts. *Deep Sea Research*, **21**, 786–789.
- Wagner, G. (1905). On some movements and reactions of *Hydra*. *Quart. J. Microsc. Sci. (N.S.)*, **48**, 585–622.
- Weill, R. C. (1934). Contribution à l'étude des Cnidaires et de leurs nématocystes. 1. Recherches sur les nématocystes (morphologie, physiologie, développement). *Trav. Sta. Zool. Wimereux*, **10**, 701.
- Westfall, J. A. (1969). Nervous control of nematocyst discharge: chemical synapses. *Am. Zool.* **9**, 1141.
- Westfall, J. A. (1970a). The nematocyte complex in Hydromedusan *Gonionemus vertens*. *Zeitsch. Zell. M. Anat.* **110**, 457–470.
- Westfall, J. A. (1970b). Ultrastructure of synapses in a primitive coelenterate. *J. Ultrastruct. Res.* **32**, 237–246.
- Westfall, J. A., Yamataka, S. and Enos, D. (1971). Ultrastructure evidence of polarised synapses in the nerve net of *Hydra*. *J. Cell. Biol.* **51**, 318–323.