THE SWIMMING RESPONSE AND ITS PACEMAKER SYSTEM IN THE ANEMONE *STOMPHIA COCCINEA*

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The swimming behaviour of the anemone *Stomphia coccinea* Müller has been de-scribed by several authors (Stephenson, 1935; Yentsch & Pierce, 1955; Sund, 1958; Wilson, 1959; Hoyle, 1960; Robson, 1961). Specimens from the region of Puget Sound and the San Juan Islands respond to contact with certain starfish or to suitable electrical stimulation with a characteristic sequence of activity. They retract, re-expand, detach from the substratum, and display a series of abrupt bending movements which may continue for several minutes. An inert recovery period is followed by re-attach-ment to the substratum. The only species so far known to provoke this response are the starfish *Hippasteria spinosa* Verrill and *Dermasterias imbricata* Grube. The world distribution of the genus *Hippasteria* overlaps to some extent that of *Stomphia*, which is a widespread North European–Arctic form, but *Dermasterias* is strictly indigenous to the north-west American coast. Neither starfish seems to affect the anemone in any other way, and the significance of this particular response is difficult to understand.

It is thus of especial interest that K. W. Ockelmann* has now found that *Stomphia coccinea* from the Öresund–Kattegat region will swim in response not only to *Hippasteria phrygiana* Parelius but also to *Aeolidia papillosa* L. Since the nudibranch will feed on *Stomphia* and occurs in the same habitat, the swimming behaviour can be regarded as an escape reaction to predators which is also evoked by certain starfish. This interpretation seems valid as *Aeolidia* has been reported from the Pacific (Abbott, 1954; but see Pruvot-Fol, 1954). A preliminary comparison of the responses to *Aeolidia* and to *Hippasteria* suggests, as will be seen, that the sensory pathways involved may be different in each case. Both stimuli are able to excite a pacemaker system which is active during swimming.

MATERIAL AND METHODS

Most of the present observations were made at the Marine Biological Laboratory, Helsingør, Denmark. Material was obtained from Knähaken (just south of Helsing-borg) by dredging at 27 m. As in Puget Sound, *Stomphia coccinea* commonly occurs on shells of *Modiolus modiolus*, and both habitats appear to be similar in other respects (see Sund, 1958; Brattströmm, 1941). One specimen of the rare *Hippasteria phry-giana* and five *Aeolidia papillosa* were also available. These and some of the anemones were kept in circulating sea water at 12° C. Other anemones were kept in bowls at 10° C., as this temperature approximated better to that of the habitat (annual range 5–12° C.).

* Unpublished observations.

Living specimens of *Stomphia coccinea* from Knāhaken closely resemble those from
Puget Sound. Dr Cadet Hand has kindly compared fixed specimens from both locali-
ties and finds them to be identical (personal communication).

Details of methods not given below have already been described (Robson, 1961).

THE RESPONSE TO *AEOLIDIA PAPILLOSA*

The specificity of response to the starfish *Hippasteria phrygiana* and the lack of
effect of *Crossaster papposus* and *Solaster endeca* from the same habitat are easily
demonstrated, and confirm Sund's observations on Puget Sound material (1958).

Table 1

| | Swimming response | | | | No. of anemones |
	+	partial	−	Trials	tested
Hippasteria phrygiana	8	2	0	10	10
Crossaster papposus	0	0	10	10	10
Solaster endeca	0	0	10	10	10

Tests were carried out in fresh sea water at 10° C. In each case the aboral surface
of the starfish was in contact with the crown of tentacles for 60 sec., although with
Hippasteria a response is usually seen after about 10 sec. Fig. 1 A shows an activity
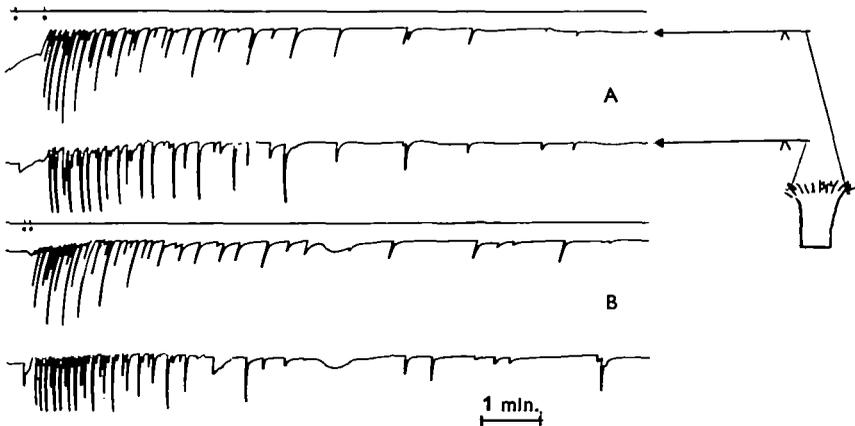record of swimming evoked by *Hippasteria*.

Fig. 1. Swimming responses of a fixed anemone recorded from threads attached to opposite
points of the disk. A. *Aeolidia* in contact with the column. Dots on the upper tracing mark
duration of stimulus. B. *Hippasteria* in contact with tentacles. Dots again mark duration of
stimulus.

Swimming due to *Aeolidia papillosa* follows the same pattern (Fig. 1 B), although
as will be seen the initial response is different. A nudibranch about to feed on one of
the anemones approaches it at ground level and the foot makes contact with the
lower part of the column. The *Aeolidia* usually secures a hold by biting deeply into
the anemone, neatly puncturing the lower part of the column, whereupon the anemone
retracts vigorously. It may then expand and swim, often shaking off the mollusc,

Frequently, however, the anemone swims before the nudibranch has bitten it, showing that contact between the foot and the column is an effective stimulus. This is the only explanation for the rapid response of some totally retracted anemones after an *Aeolidia* had crawled over them for less than half a minute.

An interesting feature of this response is that it does not usually involve the anemone's tentacles or sphincter. With *Hippasteria* and *Dermasterias* a contraction of sphincter and retractor muscles precedes swimming, but *Aeolidia* often produces no such retraction. The cerata do not evoke a response, nor does contact between any part of the mollusc and the anemone's tentacles. The nudibranch in fact withdraws if it is stung by nematocysts. All observations suggest that a substance produced particularly by the anterior part of the foot (i.e. in the region of the slime groove) causes swimming when applied to the column.

The substance produced by *Aeolidia* is chemically specific. *Aeolidiella glauca* L., a similar nudibranch from the same habitat, does not cause swimming in *Stomphia*, nor do *Armina lovéni* Bergh or the large *Tritonia hombergi* Cuvier, as may be seen from the following tests.

Table 2

	Swimming response				No. of anemones
	+	partial	−	Trials	tested
Aeolidia papillosa	76	40	30	146	53
Aeolidiella glauca	0	?3	30	33	32
Armina lovéni	0	0	10	10	10
Tritonia hombergi	0	?3	7	10	10

Tests were carried out in fresh sea water at 10° C. A negative response was recorded only after the mollusc had crawled over the column of an anemone or had been held in position for 2 min. or longer.

These results accord with the feeding habits of the nudibranchs. *Aeolidiella glauca* appears to feed mostly on *Sagartia* sp., whereas *Aeolidia papillosa* appears to prefer *Stomphia* to *Metridium* or *Tealia* and rarely takes *Sagartia*, at least in the Danish Sound (K. W. Ockelmann, unpublished observations, and personal observation; see also Stehouver, 1952; Braams & Geelen, 1953; Miller, 1961). *Tritonia hombergi* normally browses on *Alcyonium digitatum* (Alder & Hancock, 1845).

Simple aqueous extracts of the chemical substances produced by *Hippasteria* and *Dermasterias* will make *Stomphia* swim even in the absence of a mechanical stimulus (Ward, 1958; Robson, 1961), and a similar extract was therefore prepared from one of the *Aeolidia*. The head and foot, cerata, and remaining part of the body were treated separately. The tissues were fragmented with a razor blade, and ground by hand with 3–4 ml. sea water. Centrifuging at 5000 r.p.m. for 10 min. then produced a slightly turbid supernatant fluid which was used for testing. Preparation took less than an hour and the extracts were kept over ice. They were tested on anemones in dishes of clean sea water at 10° C., the extract being delivered 1–2 cm. above the expanded disk and tentacles with a pipette. Results are summarized in Table 3.

It may be concluded that *Aeolidia* produces a chemical substance causing swimming, but that it is probably not the same as the substance found in *Hippasteria* and *Dermasterias*. From Ward's account (1958) starfish extract is inactivated by boiling and

dialysis, which was not the case here. Starfish extract also produces a rapid sphincter contraction (Robson, 1961), which was conspicuously absent in most of the tests with *Aeolidia* or the extracts. As will be seen, it is probably a case of two substances acting at different receptor sites in the anemone.

Table 3

| *Aeolidia* extract	Test	No. of drops	Response
A. Foot and head	Fresh extract	5 or 10	Vigorous swimming
	After 15 min. over boiling water	5	Vigorous swimming
	Boiled over flame for 2 min.	5	Vigorous swimming
	Dialysed 26 hr. against running sea water at 12° C.	10	Fairly vigorous response
	Control kept 26 hr. at 4° C.	10	Vigorous swimming
B. Cerata	Fresh extract	40	Disk swells, mouth opens, swimming response absent
	Fresh extract B followed by extract A (control)	15 10	Negative response as above but control extract produces vigorous swimming
C. Remaining tissues	Fresh extract	5 or 10	Partial or full swimming response but less vigorous than extract A
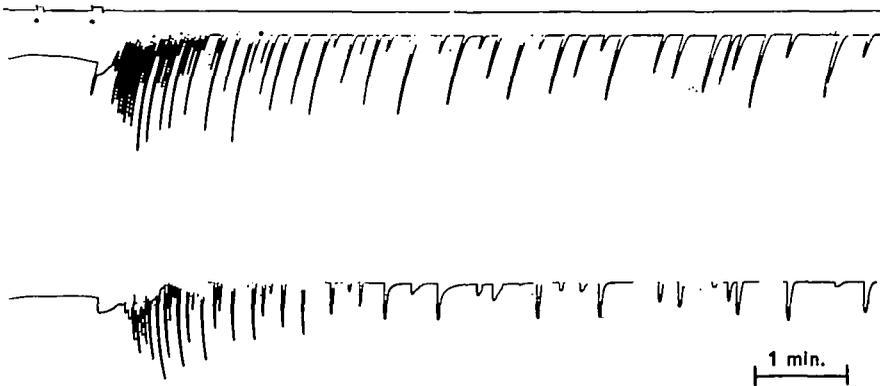
Fig. 2. Swimming response of a fixed anemone to extract of *Aeolidia* head and foot (p. 687). Dots on the upper tracing mark the addition of five and then seven drops of fresh extract near the oral disk.

Fig. 2 gives some idea of the swimming movements produced by the extract of *Aeolidia* head and foot. It is part of a kymograph tracing in which the activity of a fixed anemone is recorded by means of two threads at opposite points on the disk (cf. Fig. 1). Very similar records are obtained with *Dermasterias* extract (Robson, 1961), but a direct comparison of starfish and nudibranch extracts has not yet been made. If, however, an anemone is stimulated several times with *Aeolidia* until finally no

response occurs on contact with the mollusc, stimulating the tentacles with *Hippasteria* may still evoke quite lively swimming movements.

This suggests not only that the response to repetitive stimulation with *Aeolidia* falls away because of sensory adaptation or fatigue, but also that the nudibranch and starfish chemicals act on different sensory regions of the anemone. Since *Aeolidia* appears to stimulate the column directly, a curious anatomical problem arises. Sense cells in the ectoderm must transmit excitation to the endodermal elements which carry out the swimming response. But in sections of *Stomphia* no evidence that the processes of sense cells or nerve cells cross the mesogloea of the column from ectoderm to endoderm can be found. It remains possible that ectodermal sense cells in the column excite endodermal elements via the pedal disk. The parieto-basilar muscle fibres are unusual in penetrating the mesogloea of the pedal disk as far as the ectodermal epithelium, and could thus provide a possible anatomical pathway for the processes of sense cells or nerve cells linking ectoderm and endoderm (Robson, 1961).

Histological study of *Aeolidia* has not so far elucidated the nature or source of the stimulating substance. The anterior part of the foot appears to be more effective than the rest, and the only special gland in this region is the anterior pedal gland, which discharges along the pedal groove. Similar subdermal gland cells are also distributed over the whole pedal surface. These cells all appear to produce a continuous secretion containing mucopolysaccharide, and until further evidence is obtained, they are perhaps the most likely elements to be concerned. There are, however, at least three other types of gland cell in the pedal epithelium. In the material available it is difficult to distinguish their different phases of secretion, and the problem awaits further investigation (see, however, Campion (1961)).

THE NATURE OF SWIMMING ACTIVITY

Once the swimming activity evoked by starfish, *Aeolidia* or electrical stimulation is set up (Yentsch & Pierce, 1955; Wilson, 1959; Hoyle, 1960), it is independent of further stimulation and may continue for several minutes. The column elongates, owing to contraction of the circular muscle, and undergoes a series of stacatto bending movements brought about by contractions of the parieto-basilar muscles. It was suggested in a previous paper (Robson, 1961) that the synergic activity of these two sets of muscles is maintained locally on the column, and that parieto-basilar contractions were due more probably to a pacemaker system than to sensory or nervous reflexes. Evidence that a pacemaker system is present has now been obtained by considering the orientation of bending movements in relation to the position of the initial stimulus, and their resumption after swimming has been interrupted.

When the orientation of bending movements is observed in a swimming anemone, the alternation of parieto-basilar contractions at opposite radii is usually seen to be modified by a slow migration of the sites of excitation round the column. This slow rotation (about once a minute) does not seem to be an active process, since it can reverse in direction and may not be established until after some initial oscillation has taken place. It indicates, however, the functional equivalence of all the parieto-basilar elements in the column (Robson, 1961). It is therefore not surprising that the first

movements are orientated according to the position of the initial sensory stimulus. Detachment of the pedal disk from the substratum usually proceeds from the stimulated radius. The first parieto-basilar contraction is usually also at this radius, and thus depends on which tentacles are in contact with a starfish, or which region of the column is stimulated by *Aeolidia*. A strictly local parieto-basilar contraction also results from gently prodding the column in both *Stomphia* and *Tealia* (cf. the rapid parietal response in *Bunodactis* described by Pantin & Vianna Dias (1952 a)), and it is thus the prolonged repetition of bending movements at sites which apparently need be little related to the initial stimulus that is unusual in *Stomphia*.

The pacemaker system

A swimming anemone retracts to a sharp prod, but as the sphincter and retractor muscles relax, swimming is resumed (Wilson, 1959). It is known that halves of anemones transected during swimming continue to swim, and that both vertically divided portions and horizontally divided portions of anemones can respond to stimulation with *Dermasterias* (Wilson, 1959; Robson, 1961). When a vigorously swimming anemone is cut into two vertical halves, the halves presently relax, elongate once more and both proceed with the interrupted series of parieto-basilar contractions. If this operation is done while carefully observing the bending sequence up to the time of cutting, it is found that the first parieto-basilar contraction seen in the separated halves is always at the site that would have been expected were the anemone still intact. This makes it clear that the anemone must possess some kind of pacemaker system, and that swimming movements do not arise as a series of sensory reflexes.

The pacemaker system has been localized in an equally crude manner by cutting swimming anemones horizontally. If the transection is made one-third from the base of the column, only the upper portion resumes swimming. If the cut is one-third from the top of the column, the basal portion only resumes swimming. The pacemaker system is thus in the middle third of the column, and may be totally inactivated if a horizontal cut happens to hit on the right latitude about halfway up the column. It may thus be visualized as a circular zone of nervous activity in the column which excites the parieto-basilar muscles locally. This is shown also by a transection oblique to the main axis of the column: the two portions resume parieto-basilar contractions only in those sectors containing the pacemaker ring.

The pacemaker system can be excited either by local sensory stimuli anywhere on the crown (starfish) or on the lower column (*Aeolidia*), or by suitable electrical stimulation. Hoyle (1960) has noted that the position of electrodes on the column is important, and present observations confirm that the pacemaker system seems to be excited only by shocks delivered in its vicinity, Hoyle found that the local parieto-basilar contractions are produced by single electric shocks. It is thus simplest to suppose that during swimming each parieto-basilar contraction is due to one impulse in the pacemaker system. Electrical stimulation sometimes produces swimming movements without affecting the circular muscle. Thus the customary elongation of the anemone during swimming probably does not depend on the pacemaker.

Inspection of swimming records has failed to reveal any clear-cut patterns of rhythm beyond the exponential decline of parieto-basilar contraction frequency in any

esponse (e.g. Figs. 1, 2). The pacemaker ring fires off at numerous sites during swimming. These are all potentially labile in position, and usually do not fire regularly. The activity of the system is nevertheless integrated as a whole, and it would seem that excitation in any part of the ring to some extent influences the rest. This is seen particularly in the swimming response of isolated vertical halves. In such preparations sites of contraction do not migrate as readily as in intact anemones (p. 689), and it is usual for contractions to take place at a few radii only. Timed records from preparations show that parieto-basilar contractions at 2, 3 or 4 radii occur in fairly random order, but sometimes a statistically non-random series appears which can be interpreted as rhythmical activity at those focal points. If a recurring interval between contractions at two different radii becomes short, temporary synchronization may develop. This points to the integration of activity within the pacemaker ring since the rhythm of two or more centres is modified.

It has been noted previously that in intact anemones two contractions following at a short interval tend to occur at diametrically opposite radii (Robson, 1961). If an impulse at radius X were followed by a period of decreased probability of excitation, the most probable radius of firing during this period could reasonably be at the diametrically opposite radius Y. In fact the rapid sequence at the beginning of a response often consists of a sustained XY series, which only later includes or moves to other radii. If recent impulses can influence the position and timing of subsequent ones, both positive and negative effects may be expected. Other parts of the nervous system can also modify pacemaker activity since, for example, swimming can be interrupted or slowed down by stimulation of the sphincter-retractor system (p. 690). It seems that the appearance of leading radii in certain sequences may derive from particularly excitable sectors of the pacemaker ring, or else from the asymmetrical position of the initial stimulus.

It is to be hoped that future histological work may reveal nerve cells in the column corresponding to the position of the pacemaker ring. In the meantime it appears that swimming in *Stomphia* has several features in common with rhythmical activity of nervous origin in certain other invertebrates.

DISCUSSION

In most other sea anemones any rhythmical activity is usually far too slow to have originated in the kind of pacemaker system present in *Stomphia* (Batham & Pantin, 1950*a*, *b*; Ewer, 1960; Robson, 1961). The comparably rapid movements of *Boloceroides* and *Gonactinia* which are reported to swim have not yet been studied. There are, however, similarities in the better known locomotory rhythm of medusae, which originates in the marginal ganglia. The eight or more ganglia are connected by a nerve ring (a specialized through-conducting region of the subumbrellar nerve-net), and give rise to rhythmical pulsation of the bell. Isolated portions of this system each beat at different rates, and more slowly than the intact medusa (Horstmann, 1934*a*, *b*). They normally give a much more regular and prolonged rhythm than is ever seen in a swimming *Stomphia*. But, as in *Stomphia*, extrinsic sensory or nervous excitation can either accelerate or inhibit the pacemakers. Although the pacemaker ring is much more loosely organized in *Stomphia* than in medusae, both exhibit similar properties

attributable to the cnidarian nerve-net (see Horridge, 1955*a*, *b*; 1956*a*, *b*; 1959, Pantin & Vianna Dias, 1952*b*).

Swimming activity in *Stomphia* also has something in common with the long after-discharge of luminescent flashes produced by the sea-pansy *Renilla* when stimulated vigorously (Nicol, 1955*a*, *b*) and by *Leioptilus* (Davenport & Nicol, 1955). Strong mechanical stimuli produce a train of luminescent waves across the colony which arise rhythmically from the stimulated area. The nerve-net in which they are propagated is diffuse, and shows non-polarized through-conduction. Prolonged electrical stimuli may raise the general level of excitation until numerous local pacemakers are established, each setting up waves of scintillation for anything up to 30 min. Two other observations on sea-pens are of interest. In *Pennatula*, if waves of luminescence travelling in opposite directions meet, they tend to summate but do not pass each other at the junction (Panceri, 1872), suggesting that excitation arriving from more than one source may produce inhibition in a region of the nerve-net. This agrees with observations on medusae (Horridge, 1955*b*, 1956*a*) and probably occurs in *Stomphia*. Secondly, although at low frequency several shocks are required to initiate luminescence in *Renilla*, the effect of the first few may sometimes be seen as small flashes at points scattered all over the colony. Nicol (1955*b*, 1960) interprets this as the random distribution of photocytes with particularly low thresholds. It is evidence that in this system some of the effector cells at least are hyperexcitable. In considering the nervous organization of temporary pacemakers, it is difficult not to assume that some comparable heterogeneity exists.

Nicol (1953, 1954) has also examined luminescence in polynoid worms. In isolated scales one electric shock gives rise to a rhythmical train of flashes which depends on the presence of the elytral ganglion. When the ganglion is absent, one shock produces only one flash. The temporary rhythm must thus arise from interaction between excited nerve cells. A similar conclusion has been reached by Horridge (1957) in considering the behaviour of certain alcyonacean colonies. The response of a colony of *Sarcophyton* zooids to electric shocks, although not rhythmical, is cumulative with respect to frequency and number of stimuli. Horridge explains this by suggesting that the excitation interacts with itself until a point is reached at which the activity is self-maintaining. Although the idea refers here to the establishment of through-conduction, it appears to hold in general also for any rhythmical system set in motion by electrical stimulation. Another colony, *Heteroxenia*, shows continuous rhythmical activity of all the polyps (Horridge, 1956*c*), but since no two polyps are co-ordinated, it would seem here as though each had its own pacemaker.

There are other cases in which a pacemaker is known to reside in a relatively small number of nerve cells. Rhythmical activity of the pharynx in *Arenicola* arises from a pacemaker in the oesophageal wall, portions of which are radially equivalent as in *Stomphia* (Wells, 1937, 1950). Histological study has revealed a nerve plexus in this region (Whitear, 1953), which must therefore be the seat of the rhythm. By contrast, the rhythm of the heart in higher Crustacea originates in a few cells of the cardiac ganglion (Maynard, 1960). Despite their restricted localization in this case, it has been shown that pacemaker cells at times fire independently, and at times interact. This is no different from any other system showing temporary or sustained 'spontaneous' nervous activity, including the pacemaker ring in *Stomphia*.

Although many other examples could be given, those discussed above show that the swimming response of *Stomphia* could plausibly depend on the temporary excitation of a pacemaker ring, whose activity would have much in common with rhythms known in other cases to arise in a nerve-net or simple ganglion.

SUMMARY

1. The swimming reaction of the anemone *Stomphia coccinea* to *Hippasteria phrygiana* from Danish waters is identical with that of North American Pacific coast anemones to the starfish *H. spinosa* and *Dermasterias imbricata*.

2. The swimming reaction is also evoked by the nudibranch *Aeolidia papillosa*, which feeds on the anemone (K. W. Ockelmann, unpublished observations). The foot of the mollusc secretes a specific chemical which is not the same as that produced by the starfish, and probably acts at different receptor sites in the anemone. The swimming response is interpreted as an escape reaction to predators which is also evoked by certain starfish.

3. Cutting experiments show that parieto-basilar contractions during swimming arise from a pacemaker ring about halfway up the column, and not from sensory or nervous reflexes. Parts of the system are radially equivalent. Once excited by effective sensory or electrical stimuli, the pacemaker shows properties common to other sources of rhythmical nervous activity. Sites of firing are labile but influence others, and the activity of the intact system is correspondingly integrated.

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