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THE CO-ORDINATION OF THE PROTECTIVE RETRACTION OF CORAL POLYPS

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The responses to electrical stimulation of a number of alcyonarian, zoanthid and madreporarian corals are described. All groups studied except gorgonids show extensive coordination over the colony. In *Sarcophyton* (Alcyonacea) the response is typically local at first but eventually a wave of polyp retraction can be made to spread over the colony. The astraeid corals and the alcyonarian *Tubipora* have over the whole colony a through-conducting system which has refractory and neuromuscular properties similar to those found in the mesenteries of actinians. In the zoanthid *Palythoa* successive shocks produce excitation which spreads progressively farther across the colony at each shock for as many as fifty shocks at two-second intervals. The perforate corals *Acropora*, *Goniopora* and *Porites* respond to a single shock by a co-ordinated retraction of many polyps. Except in *Acropora*, it is characteristic of the perforate corals studied that stimulation at one point never spreads over the whole colony no matter how many stimuli are applied.

The responses of the individual polyps of many corals, including *Fungia*, are described, and in all there is a similarity to the column, disk and tentacle responses already known in actinians, e.g. *Calliactis*.

The concept of interneural facilitation has been analyzed by use of a working model which shows that the simple theory is inadequate as an explanation of transmission between polyps of certain species because the predicted transmission distances are either too variable or too small compared with the actual distances observed at the first electrical stimulus of the animal.

The properties of the co-ordinating systems between the polyps of the various groups of corals have been considered as variations on a common theme, conduction between units which form a network. The various stages from poor co-ordination, through progressive spread at each successive stimulus, to a through-conducting condition have been interpreted as a reflexion of increasing probability of transmission from one all-or-nothing unit of the pathway to the next unit in a population of a large number of units, only a proportion of which may be active at any one time. The units may be interpreted as neurones, as is probable in parts of a single polyp, or as small regions such as polyps within which there is normally through-conduction at the first stimulus.

Introduction

The intimate association between the polyps of any coral colony is commonly realized from a study of histological preparations, from the form of the colony as a whole, and from the disposition of the polyps over the colony. But the reactions which one polyp can initiate from the remainder are nowhere so clearly shown as by the relatively rapid co-ordination effected by the nervous system. Unfortunately the whole subject of the nervous co-ordination between the polyps of corals has been greatly neglected and the literature on the subject leads to the conclusion that there is little of interest to be discovered. The exception is the pennatulid *Renilla kölliker*i where co-ordination of the colony has been well studied by Parker (1919, 1920) and by Nicol (1955 *a*, *b*). Here the organization of the colonial nervous system is shown by the periodical peristalsis in either direction and by the waves of luminescence which run across the upper side of the rachis.

This gap in our knowledge has persisted partly from geographical factors but largely I think because any work in this field must be based upon the methods of using electrical stimulation developed by Pantin (1935*a*, *b*, *c*, *d*) for the study of the coelenterate nervous system, and since that time there has been little work of this kind on tropical coelenterates. Earlier workers, for example Duerden (1902) on Madreporaria, and Milne Edwards (1835) on *Alcyonium*, mentioned that polyps can move independently or may retract together when the colony is stimulated, but the responses were not analyzed in detail. Abe's work (1937, 1939*a*, *b*) on living corals at Paloa has not been continued. Also there are the additional factors that most madreporarian behaviour can be observed only at night when the polyps are fully expanded, and that the colonial nervous systems are generally rather insensitive to gentle mechanical exploration with a probe, which might be the usual initial test for responses.

The present aim is to provide some data derived from repetition of simple experiments with a variety of species. It will be shown that the interpretation in terms of the familiar through-conducting pathways and interneural facilitation, which is at present valid within individual polyps, is found to be not completely adequate for an explanation of the transmission of excitation between polyps. In addition, the concept of a through-conducting system loses its sharp outline. For example, it is possible for a system to be through-conducting at the first stimulus for only a limited, but relatively large, distance round the point of stimulation. The theme derived from the catalogue which is essential for a comparative study is the variation of the spatial spread of excitation as a result of different numbers of electrical shocks, and based on these results is an examination of the concept of interneural facilitation.

Material and methods

All observations refer to living material collected during a visit of two months (August to October 1955) at the marine laboratory of Cairo University at Ghardaqa on the Red Sea. The colonies were collected by diving and were observed fully expanded in aquaria and dishes in the laboratory. Fresh material was used daily.

The experiments were of the simplest kind. The electrical stimulation was based on the discharge of a condenser as described by Pantin (1935*a*). With most of the Madreporaria it is necessary to work during the night with only a dim light, for only then do the polyps show complete expansion. This is essential, for in general, excitation is transmitted less readily across partially contracted colonies.

Many of the observations are records of the progressive spread of excitation across the various colonies in response to successive shocks at short regular intervals. The numbers of polyps which begin to retract have been recorded for each shock. These numbers can only be approximate as they were recorded visually. In many examples the numbers of polyps were counted afterwards in areas that had been marked out on a rough sketch. The larger numbers are estimates made by multiplication of the dimensions by the number of polyps per unit area. Although accurate only to ± 20 % the results provide sufficient record of the relevant observations. On account of the variation between colonies of the same species the responses of one representative colony have sometimes been used to illustrate the characteristics of the results obtained from several different colonies, which differ slightly among themselves (as in figures 3, 5, 8, 19, 20). The general shape of the curve, which is consistent for each species, is all that is required at present. There was insufficient time available to explore the variations between individuals, and it is felt that such a study is outside the scope of the present comparative survey of the co-ordination of retraction of the polyps.

The classification of orders and subclasses used by Hyman (1940) has been followed largely because it will be the most familiar to English readers, although there have been recommendations (Stiasny 1939) for the revision of the orders of the Octocorallia.

SUBCLASS OCTOCORALLIA (ALCYONARIA), ORDER GORGONACEA

Acabaria pulchra Hickson

This beautiful little gorgonid (figure 1) was abundant under stones round the laboratory. The transparent tentacles react separately to a light touch and excitation from stronger stimuli spreads round the disk to neighbouring tentacles (figure 1*b*) and finally the polyp closes completely and retracts symmetrically. It appears from the reactions that each tentacle acts as a unit within which there is through-conduction, and between which there are junctions normally non-conducting below a threshold frequency. Also excitation readily breaks into the column where the symmetry of the retraction again indicates a through-conducting unit.

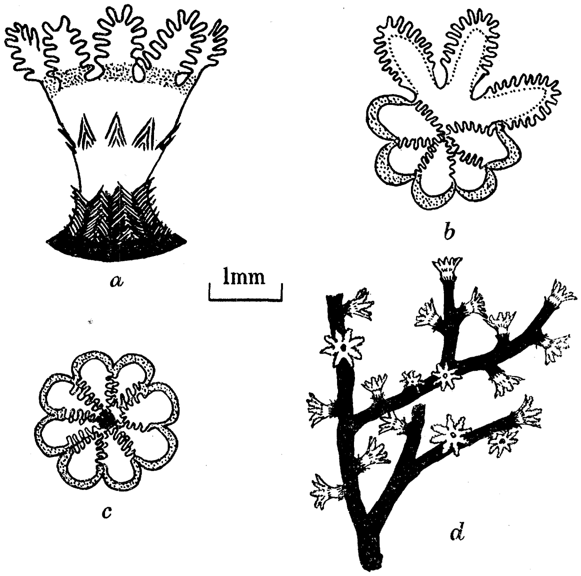

FIGURE 1. *Acabaria pulchra*. *a*, expanded polyp from the side. *b*, the disk of a polyp with five of the tentacles bent over the mouth in response to a touch to one of them. *c*, all eight tentacles contracting over the mouth. *d*, the form of a colony.

There is little co-ordination between neighbouring polyps. Twenty or so shocks at 2/s applied to a retracted polyp eventually initiated the retraction of polyps up to a centimetre along the stem. This agrees with Parker's (1925) conclusion that in gorgonids there is little co-ordination between polyps. It seems probable to me that it was this disappointing result with gorgonids that led Parker to discontinue his series of experiments upon the nervous system of colonial coelenterates.

ORDER STOLONIFERA

Tubipora musica E.H. & Sol.

A colony of *Tubipora* remains fully expanded day and night in an aquarium with hardly a spontaneous movement, except that single tentacles give an occasional jerk. When the tip of a tentacle is touched gently with a probe it rapidly bends inwards over the mouth (figure 2*b*). A small piece of mollusc digestive gland presented to a tentacle is pressed against the mouth, which opens widely. If other tentacles are affected by this process they respond by similarly bending inwards. The food is never rejected, as is always the case with the related xenids, and if the polyp is stimulated to retract suddenly while feeding it does not blow out the food despite the extra pressure set up within the coelenteron. During feeding movements there is no sign that excitation spreads by conducting pathways to neighbouring polyps.

If one tentacle is pricked delicately with a mounted needle it alone contracts and does so by shortening and becoming thicker and stiffer. The movement is quite distinct from the movement in response to a food stimulus. It is difficult to administer a prick just hard enough to evoke a response from a single tentacle. Sometimes two neighbouring arms contract, but usually there is a single symmetrical concerted jerk by all eight tentacles. This is shown by comparison of figure 2*a* with figure 2*c*. The tentacles are blown out again under internal pressure within half a minute or so. A prick administered to the side of a disk is followed by the symmetrical response of all tentacles, but in contrast with this a prick on the edge of the mouth is followed in addition by an immediate symmetrical contraction of the column (figure 2*d*). When one side of the column is gently prodded with a seeker the response is asymmetrical as in figure 2*e*, which contrasts with the symmetrical response to the second of two electrical stimuli at this point. In the above reactions repetition of the stimulus is followed by complete retraction, first of the tentacles, then of the whole polyp as in figure 2*f*.

The neighbouring polyps are never affected by such mechanical stimulation as described above, and even when about twenty polyps are made to retract individually by prodding each one down the excitation does not spread to unstimulated polyps. In contrast, when an expanded polyp is quickly beheaded with scissors all the colony immediately retracts. With an estimated velocity of 15 to 20 cm/s a series of waves of retraction spread over the whole colony, each wave consisting of a symmetrical retraction of the polyps in turn. The waves spread in all directions and usually succeed each other at about 2/s. The polyps stiffen and shorten their tentacles then progressively retract in a series of discrete jerks. As a result of the movement there is a startling colour change from the yellowish green of the tentacles to the reddish purple of the corallite.

The effects of electrical stimulation were studied by means of a small electrode clamped in a position to stimulate the disk of an expanded polyp. There is a definite threshold of intensity below which no effect follows several shocks. Above this threshold a single shock is followed by no visible response except a waving of some of the tentacles, both in the stimulated polyp and also in distant parts of the colony. However, at the second of two shocks, interval 1 s, a wave of polyp retraction spreads over the colony (or at least a large part of it) involving many hundreds of polyps. The response is similar to one of the waves initiated from a wound as described above. With two shocks, interval 1 s, at different points on the colony, a similar co-ordinated retraction of all polyps follows. To be effective the interval between a pair of shocks must be less than 4 s at 26° C.

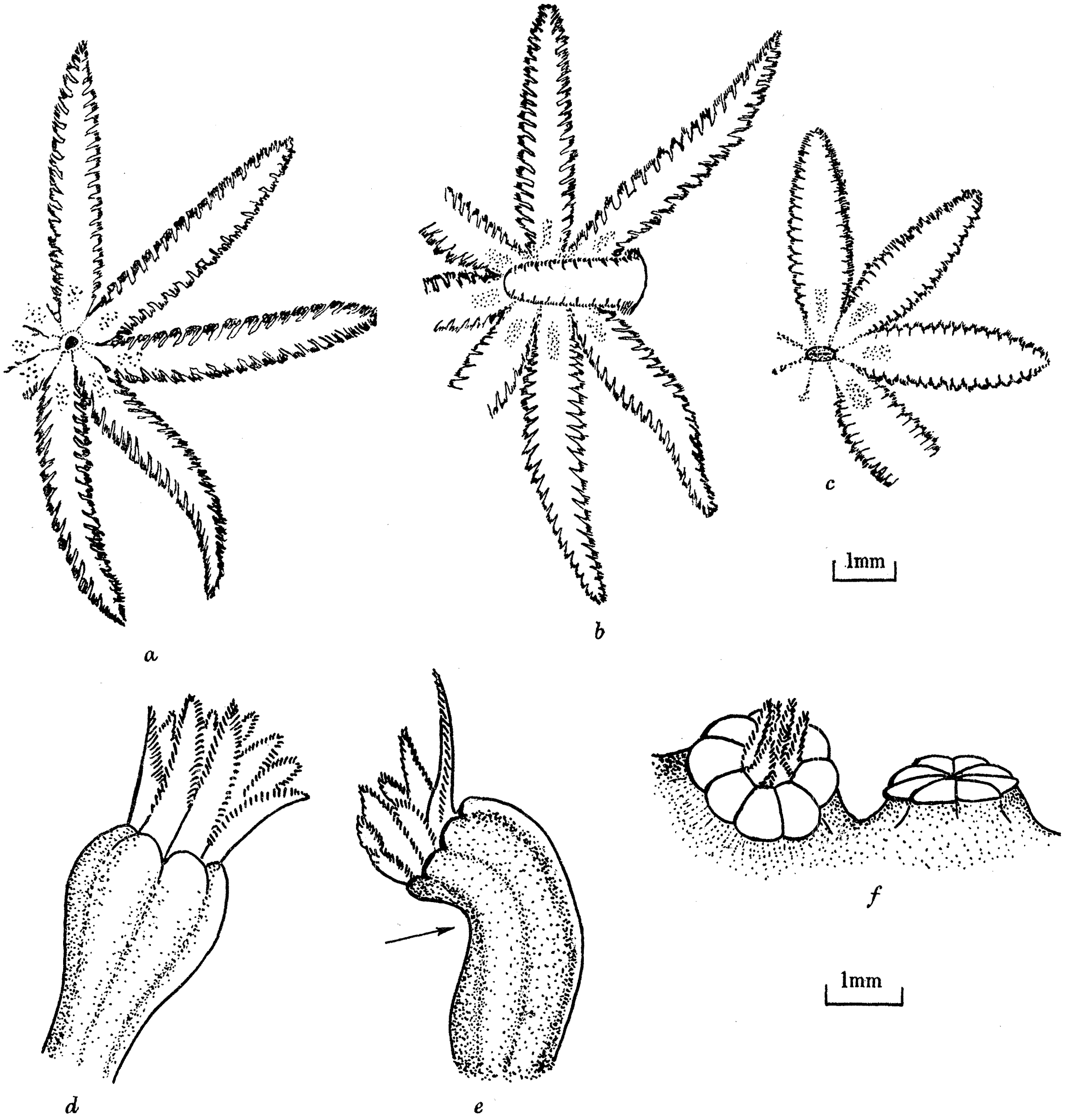

FIGURE 2. *Tubipora musica*. *a*, part of the oral surface of an expanded polyp. *b*, the response of a single tentacle to touch or to a particle of food. *c*, the symmetrical response to a sharp prick or pair of electrical shocks; in contrast to *b* the response is a shortening rather than a bending. *d*, a partially retracted polyp which has been stimulated electrically. *e*, an asymmetrical contraction of a polyp which is stimulated mechanically at the point indicated by the arrow. *f*, completely retracted polyps.

The response of the colony to further shocks cannot be represented as a progressive spread because usually the whole colony is affected by the wave following the second shock. Figure 3 shows the effect of a number of stimuli, intervals $\frac{1}{2}$ and 2 s, on the extension of a representative polyp. The values are only approximate, derived from a series of measurements against a millimetre scale.

Taking advantage of the absence of a response to the first of a pair of shocks I was able to measure the refractory period by progressively shortening the interval between first and second stimuli until the second shock no longer produced its effect. This happens at an interval of 0·02 s with stimuli at least three times threshold intensity; at intervals slightly greater than 0·02 s there is a relatively large response. The second shock may be applied at any point relative to the first with the same result, except that the refractory period now appears slightly longer on account of the transit delay. The results are consistent with the velocity of conduction as observed above, but more important, they also demonstrate that the whole conducting system is thrown into a refractory state by the first stimulus and this in turn is good evidence of a through-conducting, unpolarized transmission system in which a single impulse spreads from each applied condenser shock. This again implies a sharp physiological separation of the through-conducting system from that part of the nervous system which is concerned with the co-ordination of local responses, as in feeding.

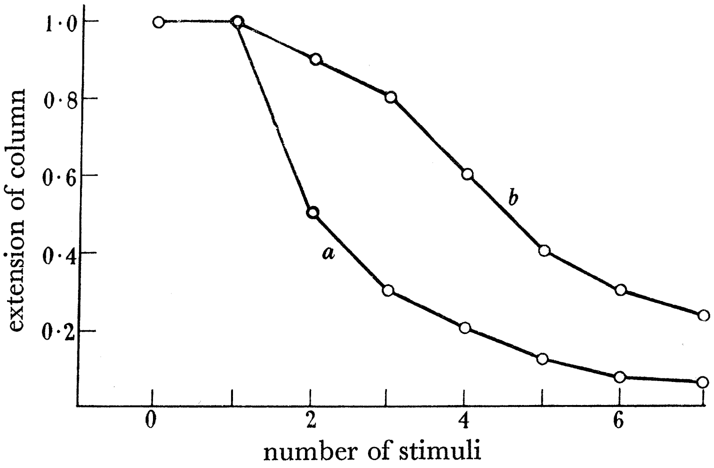

Figure 3. The approximate extent of the retraction of the column of *Tubipora* following various numbers of shocks (*a*) at $\frac{1}{2}$ s and (*b*) at 2 s intervals. The measurements were made against a millimetre scale and are only approximate.

In all these experiments with the colony conducting system of *Tubipora* the exact site of application of stimuli is of little importance. The polyp disk and wall, the tubes, platforms, and even the bases of tubes several centimetres long, are all equally points of access to the colonial conducting system. The various points are not equal in sensitivity but this topic was not analyzed.

Order Alcyonacea

Sarcophyton ehrenbergi Marenz.

Large fleshy colonies of *Sarcophyton* up to 1 m across were observed under water on the reefs and smaller colonies 10 to 20 cm across (figure 4) were studied in aquaria. These specimens, which are brownish olive with yellow or pinkish polyps (= autozooids), do not keep very well once removed from the sea and many colonies never inflated properly when collected. They cannot be removed from the stones to which they are attached because any damage is quickly followed by deflation and death, probably by failure of the water currents through the colony.

A single shock to one tentacle of a polyp is followed by the retraction of that tentacle and usually by a partial but symmetrical retraction of the column. A similar result follows a single shock on the disk or column or on the syndete at the base of a polyp. Two shocks (interval 1 s) are followed by a partial retraction of two or three of the neighbouring polyps. Three shocks (intervals 1 s) produce a movement of perhaps six neighbouring polyps, four shocks a movement of ten to fifteen, together with a complete withdrawal of the polyp stimulated. These results are summarized in the diagram (figure 5), showing the numbers of polyps influenced by various numbers of stimuli at 1/s.

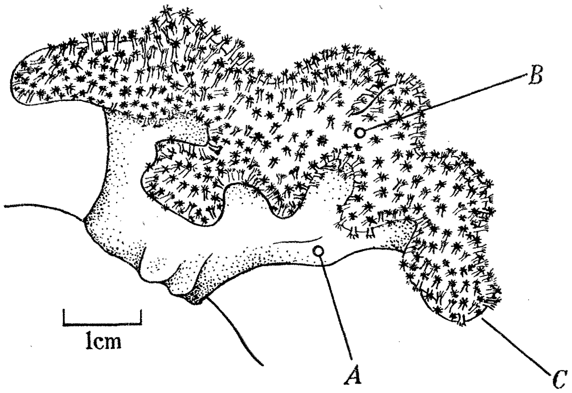

FIGURE 4. *Sarcophyton ehrenbergi*. A small colony fully expanded. A series of shocks applied to point *A* was followed by a movement of the syndete in the region *C*.

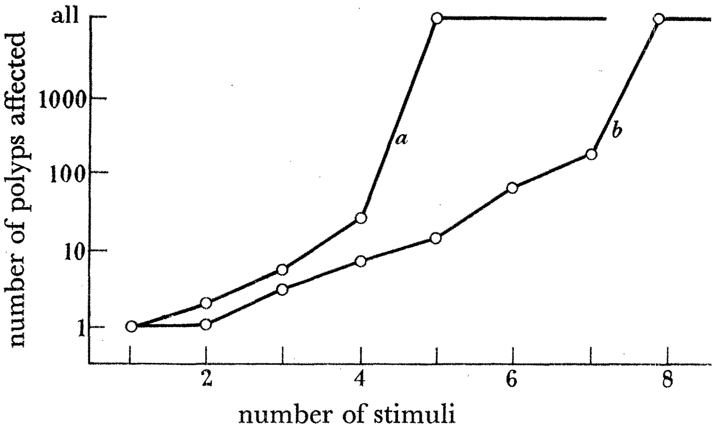

FIGURE 5. *Sarcophyton ehrenbergi*. The relation between the number of stimuli applied at intervals of (*a*) 0·5 s and (*b*) 1·0 s and the number of polyps affected. The increasing slope of such curves was typical of this species for intervals less than 4 s.

The contractions of the polyps surrounding that stimulated are slow in *Sarcophyton* compared to *Tubipora*, and it is hardly perceptible that in the movement there are discrete jerks which correspond with the arrival of the excitation from each shock. Even in response to the first stimulus the movement may continue for many seconds. This continued movement has approximately the same time course as the withdrawal of the syndete away from the electrode and the co-ordinated movements of other parts of the syndete as described below. It shows that a shock not only produces a single impulse which spreads as a wave but also initiates some kind of local maintained activity, about which more will be said in the discussion.

With longer intervals between shocks the stimulus does not spread so far over the colony. For example, with repeated stimulation at a spot between two polyps with intervals of 15 s between shocks it took five shocks before the excitation traversed 5 mm. At the sixth shock there was a movement of six polyps, and with successive shocks the number of affected polyps increased to twenty at the tenth shock, but the excitation never spread further than this, however many more shocks were applied at the same frequency.

Stimulation on the stem of the syndete, for example at *A* in figure 4, has little effect if only three or four stimuli are given, but after a series of shocks (about six at 1/s) there is a retraction of large numbers of polyps on the nearer parts of the upper surface, and in some examples a wave of polyp retraction sweeps across the whole colony. At the same time a slow movement of the syndete round the electrode begins and continues for up to a minute after the last shock. The directions of such movement fail to show any differentiated gross pathways or regularities which would pull the tissue in any particular direction. The movement of the syndete is primarily a slow contraction and deflation, which is initially localized, but which spreads over the whole colony following repeated shocks at one point.

With stimuli at 1/s the number of *extra* polyps affected by each successive shock increases rapidly. This is shown in figure 5, where the number of shocks is plotted against the number of affected polyps. Even with a logarithmic ordinate the curve bends upwards and after a certain number of shocks, usually six to twelve at 1/s, a wave of retraction spreads over the whole colony. In one example, perhaps exceptionally sensitive, six shocks applied to the syndete at *A* in figure 4 at intervals of 5 s produced a wave of polyp withdrawal. Underwater observations on the very largest colonies showed that when one edge is crushed a similar wave spreads across the whole colony, which may measure 1 m across.

There is a characteristic movement of the syndete associated with a number of such waves following frequent stimulation at any point. The syndete contracts and the edges are thrown into folds which are pulled together as the colony crumples and collapses. After 1 min all the polyps have completely retracted.

A difficulty in assessing the effects of stimulation on *Sarcophyton* is the inherent variability. There is no inconsistency in the results, for curves of the kind shown in figure 5 are always found, but the parameters differ between different specimens.

The cumulative effect of a number of stimuli is not only a consequence of their absolute number; frequency is equally important as shown by the two curves of figure 5. Also, in another experiment sets of six shocks at constant strength were given on the edge of the upper surface with 15 min periods of rest between bursts of stimuli. The response depends on the interval between the shocks of a burst as follows. Six shocks at 20 s intervals produce no effect except contraction of two or three polyps and slight local movement of the syndete. With 15 s intervals about twenty of the nearest polyps show a very slow partial withdrawal. A similar response follows if the intervals are reduced to 10 s, but with intervals of 5 s the sixth shock produces a wave of retraction over the colony and considerable later movement and folding of the syndete. As in figure 5 there is apparently a critical 'quantity of excitation' (whatever it may be) which does not die away locally but is propagated over the syndete. Further reference will be made to this in the discussion.

Subclass Zoantharia, order Zoanthidea

Palythoa tuberculosa Esper.

This is a colonial zoanthid which encrusts pieces of dead coral in shallow water. The polyps are buried nearly up to their margins in a tough, gritty coenenchyme which extends as a brownish coat over the substratum for as much as a metre. Figure 6 gives some impression of individual zooids and the form of the colony.

The reactions of individual polyps are few and simple. At a touch or electrical shock applied to its tip a tentacle quickly bends towards the mouth by a contraction of its base (figure 6*a*). Other tentacles may not be affected. A single shock to the margin or to the disk is followed by a single symmetrical jerk of the whole polyp, which closes completely after four or five further shocks (figure 6*b*). But by contrast with this symmetrical movement a gentle mechanical stimulation or a small piece of food applied to a tentacle or to the margin can initiate a local inward bending and a local movement of the tentacles as in figure 6*c*. The food is quickly pushed down the deep cavity to the disk, where the mouth opens symmetrically to receive it. The outward ciliary currents up the sides of the disk are locally reversed by food particles.

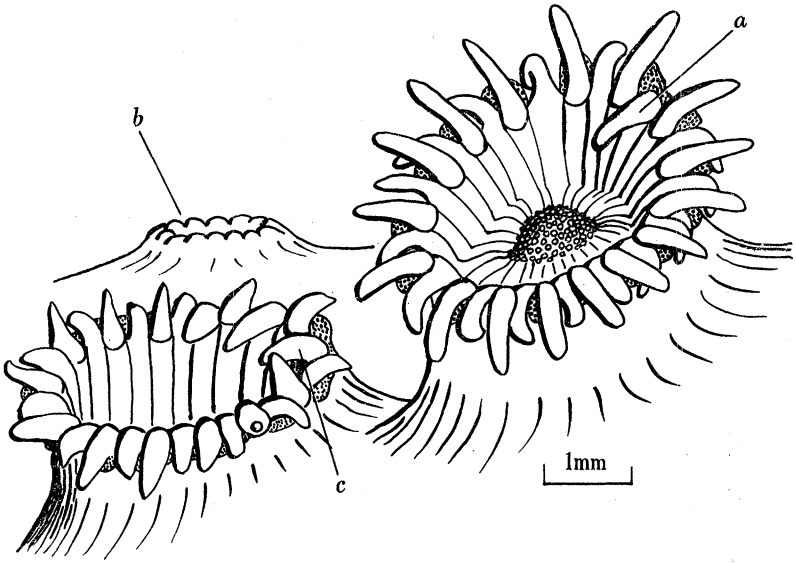

Figure 6. *Palythoa tuberculosa*. *a*, the inward bending of a single tentacle when touched. *b*, the appearance of a completely contracted polyp. *c*, the response of a single tentacle spreads round the margin of an extended polyp.

The asymmetrical movements during feeding and in response to a small mechanical stimulation are not transmitted to neighbouring polyps, though all are very sensitive to vibration of the colony. However, electrical shocks applied to a polyp or to the surface of the coenenchyme are transmitted to neighbouring polyps and eventually over the whole colony. In figure 7 is shown a particular example of this transmission. An electrode indicated by the arrow was applied to the polyp *S*, which contracted a little in response to the touch. After a pause of several minutes a single shock was given and this produced no effect. Further shocks followed at intervals of 2 s, and in the circles are shown the number of shocks required before the polyp so represented gave its first movement in response. In figure 8 is shown the relation between the number of shocks and the number of affected polyps in a long strip of the colony. *Palythoa* is quite different from the alcyonarian and madreporarian colonies here described in the great number of shocks that are required to push the excitation across several centimetres of the colony and in the relatively linear relation shown in figure 8. That the long delay is not the result of long transit times is shown

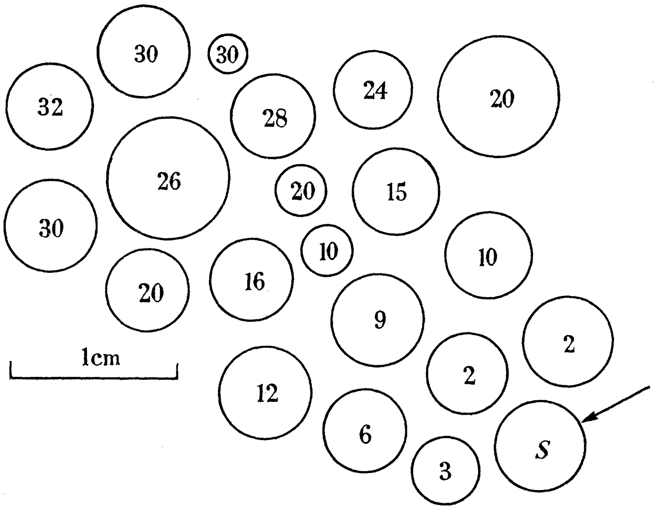

FIGURE 7. Results of stimulating a particular colony of *Palythoa* with shocks at 2 s intervals. The circles represent polyps and the numbers in the circles show the number of shocks required to initiate a first response from that polyp. The stimulus was applied on polyp *S*, as indicated by the arrow.

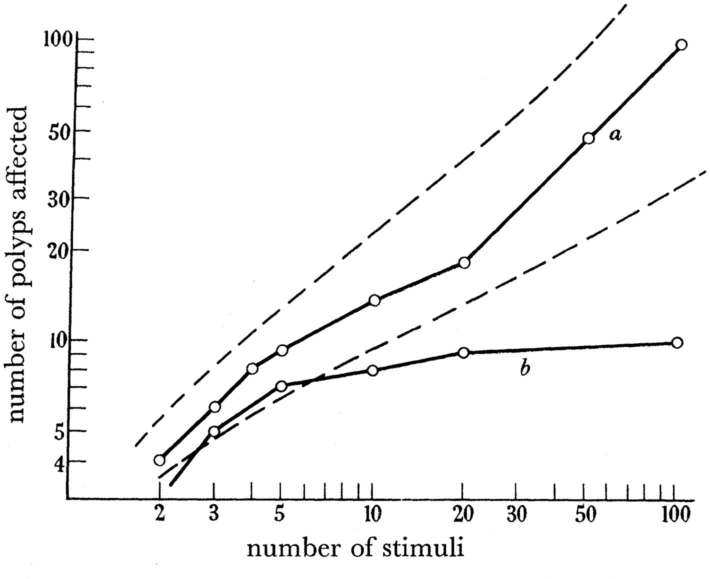

FIGURE 8. The relation between the number of shocks and the number of polyps affected in *Palythoa* at frequencies of (*a*) one shock per second and (*b*) one shock per 10 s. The dotted lines show the limits of variation between colonies in the first case.

by the sudden cessation of the distant contraction movements at the moment the sequence of stimuli is terminated. Shortening the interval between stimuli to 0·5 s accelerates the contraction of polyps near the electrodes but hardly affects the rate of spread per second over the colony. A much slower frequency at 1/10 s fails to push the excitation to more than a dozen or so neighbouring polyps no matter how many shocks are given.

SUBCLASS ZOANTHARIA, ORDER MADREPORARIA

Galaxea (sp. probably **fascicularis**)

The co-ordination between the polyps of *Galaxea* is sufficiently different from that in the other madreporarian corals studied to justify special treatment. In many respects the co-ordination is similar to that found in *Palythoa.*

Each polyp has two rings of tentacles of which the vertical ones are practically immobile since they each contain a sharp skeletal spike. Between these the alternate tentacles project sideways or contract and bend when stimulated. The polyps are sufficiently closely packed for these outer tentacles to overlap with those from the neighbouring polyps. A small mechanical stimulus or a piece of food applied to one of the second ring of tentacles initiates a typical feeding response. As indicated by the arrow in figure 9, a single tentacle may alone bend inwards between the vertical spikes, and carries the food towards the mouth, which opens to receive it. The reaction may spread round the disk to neighbouring tentacles, but in general it is not symmetrical.

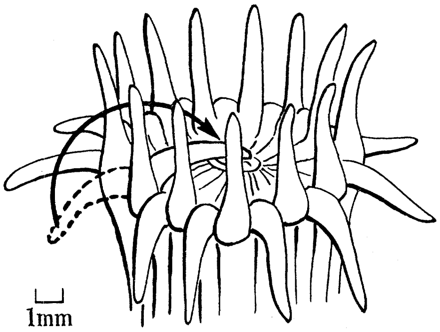

FIGURE 9. *Galaxea fascicularis.* The form of an expanded polyp. The arrow indicates the response of a single tentacle when the tip of it is touched with a particle of food.

A single electrical shock just above threshold applied to a tentacle produces a local contraction of this tentacle alone. When applied to the disk or to the living tissue between polyps it produces only a local contraction limited to a few millimetres round the electrode. There may, in addition, be a slight bending of one or two tentacles. However, when a second shock is applied within an interval of 4 s there is a rapid, symmetrical jerk of the polyp. With the electrode situated between polyps the two or three nearest ones respond to the second shock. The movement is brought about by endodermal mesenteric muscles as in anemones and polyps of other corals. At a third shock a wider area responds. With continued stimulation at 1/s the area in which polyps respond by symmetrical retraction goes on increasing up to about the 18th shock but with decreasing 'marginal value'. At each shock there is a definite co-ordinated jerk of all the polyps affected. With stimuli at 2/s the spread in area is more rapid; at 1/2 s it is slower and never reaches so great an area as at 1/s.

The relation between the number of stimuli at various frequencies and the number of polyps affected is shown in figure 10. The curves rise at a rate that depends on the frequency and each reaches its own maximum value. This maximum is reached when the stimulated area becomes saturated in some way. The mechanism of transmission has not been analyzed further but will appear again in the discussion. At a frequency of 1 shock/2 to 3 s an interesting phenomenon was noted. The jerks, normally at each shock, may suddenly stop and the polyps relax for a moment, then the co-ordination may begin again later. A short example of such a lapse, illustrated in figure 10, is probably due to a temporary fall in sensitivity at the point of stimulation. In all these experiments an increase in the strength of the stimulus has no effect unless great enough to produce an after-discharge which is, however, readily detectable. It was possible to demonstrate the existence of a refractory period, taking advantage of the discrimination between one and two shocks, but unfortunately an accurate value cannot be given.

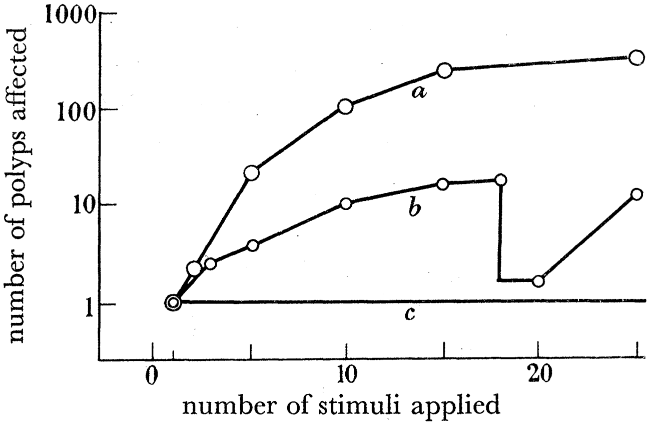

FIGURE 10. *Galaxea fascicularis*. Relation between the number of shocks (at intervals of (*a*) 1 s, (*b*) 2 s and (*c*) 4 s) and the number of polyps affected. Further explanation in the text.

Madreporarian corals of the group Astraeidae

This group of genera of the Madreporaria are classed together on grounds of skeletal similarity. This systematic relationship is borne out by the close similarity in the responses of at least those members of the group which I was able to study. There were the following species at Ghardaqa: *Echinopora ehrenbergi*, *Favia clouei*, *F. denticulata*, *F. laxa*, *F. lobata*, *F. speciosa*, *Cyphastraea savignyi*, *Goniastraea halicora* and several undetermined species of the meandrine *Coelaria*. The polyps expand in the dark, and the only illumination that could be used was a small paraffin lamp with the wick turned well down. It is an important point that the co-ordination between polyps is not so complete or so easily observed when the colonies are partially expanded.

Favia laxa Klunzinger

Although rarely recorded, this species was available on the inshore reefs at Ghardaqa, collected by diving about 4 m, and, as for the rest of the specimens, was carried to an aquarium in a bucket without exposure to the air or strong sunlight. This particular species was favoured because the polyps expand readily after stimulation, the responses were consistent and the colonies a convenient size. The expanded polyps (figure 11*a*) are beautifully transparent with very few zooxanthellae in the column or tentacles.

In response to a small particle of food a tentacle bends inwards to the mouth; at the same time the mouth begins to open and there is a local contraction of the disk, which is lowered on the side stimulated. Following continued mechanical stimulation there is a local secretion of mucus from the surface of the disk, and under normal circumstances this mucus is carried towards the mouth by cilia. Larger particles are pressed down by the tentacles. This reaction resembles the feeding reactions of *Fungia*, and many anemones and coral polyps with short tentacles, in that there is a co-ordination of the tentacle, which bends, the mouth, which opens, and the local radial movement on the disk between them. The response, though it may be sustained, is quite distinct from that which follows electrical stimulation.

For the application of electrical stimuli two small silver electrodes mounted inside capillary tubes were allowed to rest gently on the surface of the expanded colony. It was found that this adequately avoided the difficulties due to retraction of the tissue away from a clamped electrode. A number of preparations were set up and left to expand fully in darkness. The interesting result is that a single shock produces no response except a slight tentacle waving over the whole colony, or at least over a wide area, and a second shock, if applied within 4 s of the first, produces a sudden co-ordinated partial retraction. The second shock may be applied at a point distant from the first, but the result is exactly the same. The spread of the response shows that the through-conducting system of each polyp is physiologically continuous with its neighbours and that relatively large areas are thrown into a state of expectancy at the first shock and respond by a co-ordinated contraction at the second. Each of the above species of astraeids behaved in the same way; for example, a single shock to the surface of a large leaf of *Echinopora* produced only a local contraction about the electrode and the usual tentacle waving, but at the second shock (interval 1 s) a jerk of each polyp spread as a wave over the leaf or branch, affecting several hundred polyps in sequence.

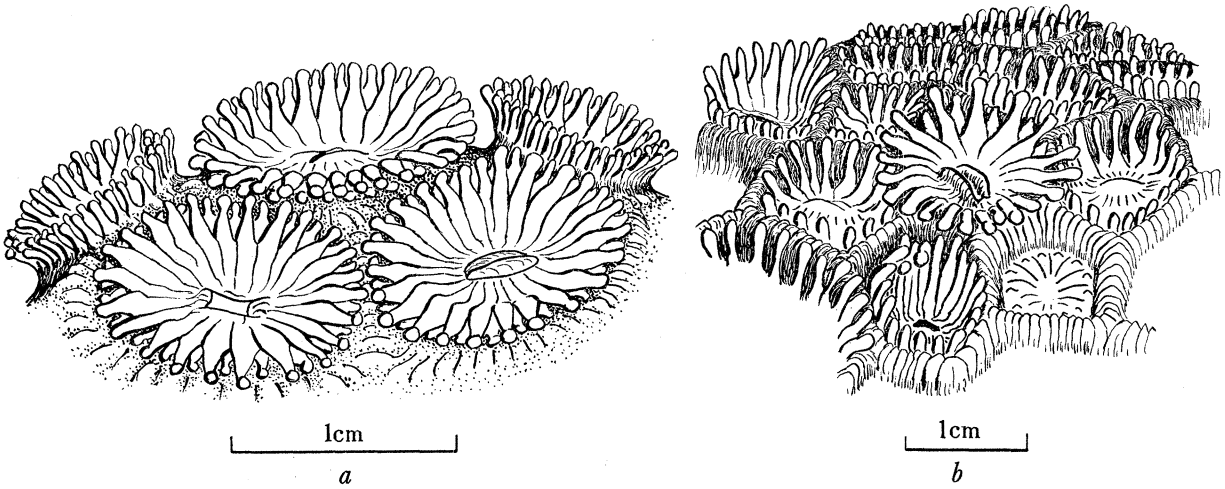

FIGURE 11. *a*, *Favia laxa*. Five expanded polyps to show their shape and the form of the colony. *b*, *Goniastraea halicora*. A group of expanded polyps to show their shape and relationships. The centre one is fully expanded and the others show various degrees of retraction.

The absolute refractory period of the colony conducting system of *Favia laxa* was measured by the standard method of reducing the interval between a pair of shocks until they no longer produced a movement. Only the waving of the tentacles, characteristic of a single shock, followed a stimulus pair with interval 0·05 s, and a number of experiments showed that the refractory period is always less than 0·09 s; most experiments gave a result of 0·06 to 0·08 s at 26° C. The second of the pair of shocks could be applied at a point 10 cm distant from the first, but the result was still the same; though, as in *Tubipora*, slightly longer refractory periods are found on account of the transit delay between the two electrodes. A similar demonstration of the refractory period was possible in the other species and no significant differences emerged.

The extent of the colony affected by the second shock varies considerably, both between species and between different states of expansion of one colony. I found with a spherical colony of *Favia laxa* 15 cm diameter that about half of the colony responded to a pair of shocks at 1 s interval, and the other half was similarly co-ordinated together when tested a little later. In the common small round colonies of *F. clouei* an area of about 5 × 5 cm comprising about thirty polyps is affected by a pair of shocks with 1 s interval. Successive stimuli push the response progressively further, but the whole colony does not necessarily react. Exactly the same situation is found in large colonies of *Goniastraea halicora* (figure 11 *b*), where initially an area of 20 × 20 cm was affected in one particular example. In *Favia lobata*, with much smaller polyps, a single pair of shocks initiate a contraction in a relatively small area of about 2 × 2 cm affecting about 100 polyps, and it takes six or so shocks at 1/s to complete the spread of excitation over a small colony 10 cm across. However, despite these minor differences between species, the colonial co-ordination of the Astraeidae is quite consistent except that it is not so complete in semi-contracted regions. This may be no more than a simple mechanical prevention of conduction by the tight contraction of tissue against the sharp ridges between polyps, but this point has not been examined further.

In *Coelaria* excitation leading to local movement of tentacles, for example, in the acceptance of food, is not transmitted across the ridges between the polyp-filled grooves, but the colony conducting system freely crosses in all directions as in *Favia*. Whatever advantage may be derived from the meandrine habit it appears to have nothing to do with the ready conduction of excitation.

In all the astraeid corals available the summation phenomena typical of coelenterate muscular responses always appeared. This is best seen by comparison of the effects of a second shock following the first at various intervals. The pairs of shocks must be well separated by periods of rest to avoid interaction. In most astraeids six or so maximum responses, following intervals of 0·2 s, complete the retraction of a polyp. At the other end of the scale a second shock after an interval of 5 to 7 s produces no retraction response at 25 to 26° C. This is comparable with values from anemones in temperate regions.

Lobophyllia (sp. probably **corymbosa**)

The relatively large polyps of *Lobophyllia* are anatomically and physiologically quite separate as shown in figure 12. Individually they react as actinians, with a local system of asymmetrical propagation round the disk, and through-conduction for retraction of the mesenteries and withdrawal of the tissues.

A slight mechanical stimulation of a tentacle or of the tissue which extends a little way down the sides of the columnar skeleton (*X* in figure 12) is followed by only a local contraction and a movement of the nearest tentacles. Food is quickly caught on a tentacle, which contracts and carries it to the mouth. A single electrical stimulus of a tentacle may produce a similar result. However, a different response follows the second of two shocks applied anywhere on the column relative to the first with an interval of 1 to 5 s. The disk gives a symmetrical jerk of retraction, the tentacles shorten suddenly without bending, and with further shocks the tentacles disappear leaving a ring of spikes thinly covered by an olive brown, tough, protective layer. On the evidence that it is immaterial where the second shock is located relative to the first, the symmetrical response appears to be effected by an endodermal giant fibre system exactly as in anemones, everywhere thrown into an expectant state by the first stimulus.

A refractory period exists but was not measured. The velocity of conduction of 8 to 12 cm/s across a polyp was derived from measurements of the delay on a smoked-drum record of retraction at opposite ends of a polyp 5 cm apart. *Lobophyllia* was the only example on which I was able to do this. It was noticed that, in a specimen with two polyps which were almost separated asexually, only a very thin bridge of the marginal tissue 3 mm wide was sufficient for continuity of the through-conducting system.

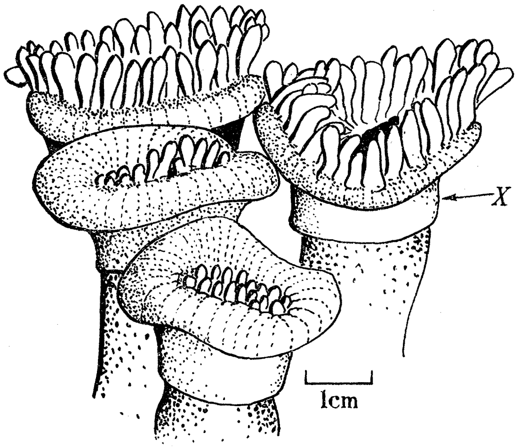

FIGURE 12. *Lobophyllia* (probably *corymbosa*). A group of four polyps in various stages of expansion, showing the complete isolation of each polyp on its separate column.

Fungia fungites L.

This is a brownish *Fungia* with relatively short tentacles as shown in figure 13. Another species, which was smaller, paler and with longer tentacles, was common at Ghardaqa. The reactions of the two species were very similar, and also casual observations on *F. dentigera* and *Herpetolitha foliosa* Ehrb. showed that the behaviour described here is common to all.

Particles of sand which fall on the surface are carried to the edge by cilia whether the animal is contracted, as in sunlight, or expanded. However, if a particle of food touches the disk, particularly in an expanded individual, there is a local secretion of mucus and reversal of the ciliary beat, which now carries the particle towards the mouth. The ciliary reversal occurs equally well at any point. At first it is localized, but a simple experiment with small partitions resting on the surface of the expanded polyp showed that it is quickly propagated through the tissue (not by diffusion through the water alone) until it has spread along the line of the septum between the food and the mouth. Neighbouring septa are not affected, except by diffusion. Complete local reversal may be evoked in fully contracted animals. In addition, there is a slight retraction of the interseptal tissue in the regions where there is ciliary reversal. The results indicate centripetal conduction which affects both cilia and muscles. There is little conduction in the centrifugal direction, towards the margin.

A single tentacle responds to a touch at its tip by bending at its base and pointing towards the mouth. When any point on the upper surface is touched by a seeker or a scrap of crab muscle two or three neighbouring tentacles bend towards it. Tentacles between neighbouring septa bend sideways tangentially to the axis of the animal as shown round the black spot in figure 13. This response spreads sideways over five or six septa. A related response is seen when food particles reach a tentacle as they move along a septum towards the mouth. The tentacle bends at its base and comes to lie along the surface, pointing towards the mouth. The ciliary current, always directed towards its tip, carries the food over the tentacle and off the end of it. This process is a logical requirement of the ciliary reversal because food may sometimes be caught on the side of a tentacle away from the mouth.

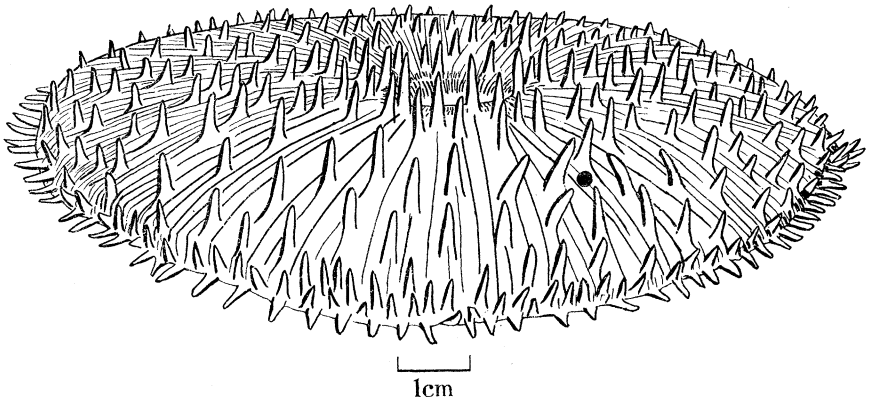

FIGURE 13. *Fungia fungites*. A fully expanded specimen of the variety common at Ghardaqa. A few tentacles are inclined towards the point of mechanical stimulation indicated by the black spot, as described in the text.

Quite distinct from the essentially local and radial feeding responses is the symmetrical retraction following laceration of the tissue or electrical stimulation of the general upper surface. As in the actinians two shocks above threshold are required and a single shock produces only a slight waving of most of the tentacles. The second shock may be at any point relative to the first and to produce a contraction must follow it after an interval between 0·1 and 5 to 8 s. The facilitation is well marked, as shown by approximate measurements of the retraction of tentacles when the second shock is applied at different intervals after the first (figure 14). When the stimuli are applied to the tentacle itself, three or four shocks may be necessary to initiate a symmetrical contraction of the rest of the animal. As the animal retracts between its septa the water in the coelenteron flows out of the mouth, which opens, apparently, only as a mechanical consequence.

The tissue of *Fungia* would not support a lever for recording on a smoked drum, so that it is impossible to give an accurate figure for the velocity of transmission across the polyp. Observations of large individuals of 20 cm diameter gave a subjective impression that the velocity is as great as 40 to 50 cm/s. It is also clear that it is the same in all directions and that the impulses freely cross peripherally between the mesenteries, i.e. are not co-ordinated only in the oesophageal region.

I was able to confirm that an individual *Fungia*, particularly when small, can move a few centimetres across the flat floor of an aquarium during the course of a night. Specimens placed upside down can turn over by the rhythmical inflation of the upper surface described by Abe (1939*b*), but I did not observe this process to completion. Specimens inverted on sand excavated a hollow by the ordinary centrifugal ciliary cleaning current. On moving up the side of this hollow, the *Fungia* would then turn over by the action of gravity helped by an incomplete inflation of the coelenteron.

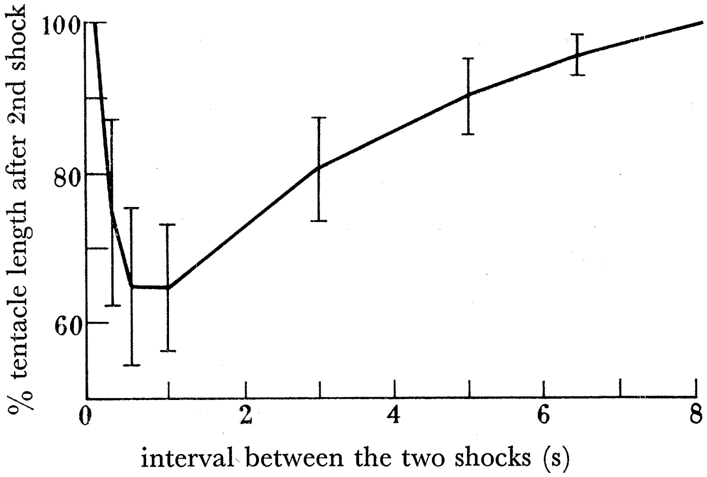

FIGURE 14. *Fungia fungites*. The relation between the interval between a pair of shocks and the co-ordinated tentacle contraction which follows the second shock of the pair. The measurements were made against a centimetre scale and are only approximate. The vertical lines show the extremes of the variation between tentacles.

Pavona and *Hydnophora*

A few colonies of the complex fungid *Pavona cactus* Forsk. were scattered about the inshore reefs at about 5 m depth. This species expands well in diffuse daylight, as in figure 15 (in which the areas dotted are darkly coloured in life). The ciliary currents towards the edges of the lamellae are well marked, and rejected particles are carried outwards over mouths that remain tightly closed. Unlike Abe (1937) I did not observe a ciliary reversal on presentation of crab muscle as food. The food particles were caught in mucus and swallowed by the next mouth in the normal outward path.

A single electrical shock applied to the general tissue surface produces a local contraction of tentacles and mesenteries for an area of about 1 cm^2 round the electrode. With further shocks the affected area is extended, but there is no sign of a through-conducting system over large parts of the colony and no special effect is observable at the second shock. After ten shocks at 1/s the maximum area of contraction was about 6 × 6 cm and included five to seven of the upright leaflets of the colony.

Pieces taken from the strange fungid *Hydnophora contignatio* Forsk. are rather insensitive to light and stimulation and remain expanded during the day, as in figure 16. Ciliary currents are consistently towards the edge of the horizontal flat leaves of the colony, along the ridges and also along the grooves where rows of tiny mouths catch any pieces of food that are carried along. The responses to stimuli are unsatisfactory. A single electrical shock produces a retraction of the surface and tentacles for a few millimetres round the electrode; repeated shocks extend the area of response to only a few centimetres with a local secretion of mucus.

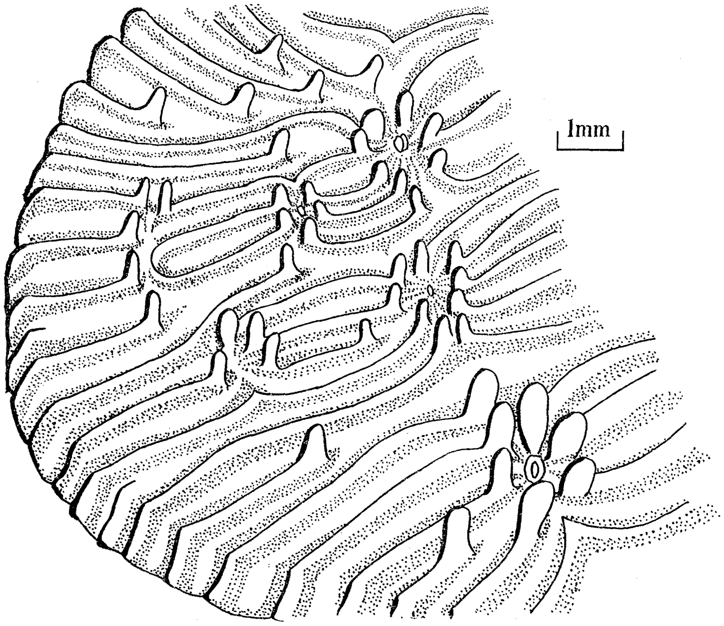

FIGURE 15. *Pavona cactus*. Part of an expanded colony showing the relationship between the polyps.

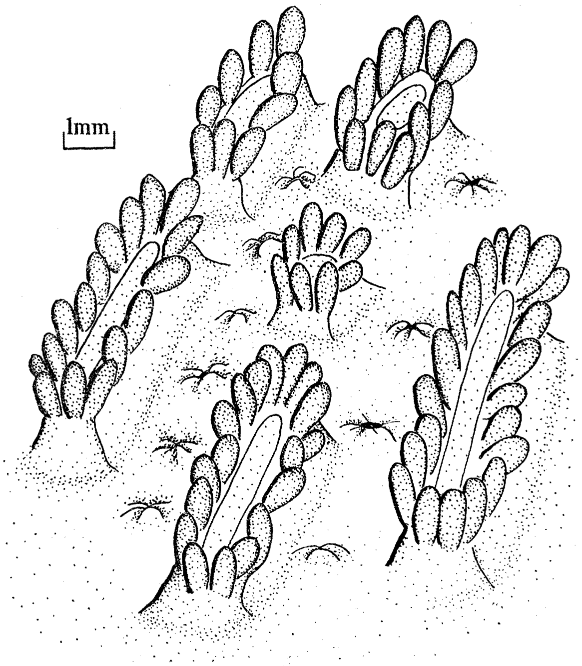

FIGURE 16. *Hydnophora contignatio*. Part of an expanded colony showing the rows of mouths in the hollows between the ridges, on which stand groups of tentacles.

PERFORATE CORALS

Acropora spp.

To the species of *Acropora* common at Ghardaqa I hesitate to apply specific names. Three of the common species are similar to Klunzinger's (1879) photographs of *Madrepora scandens* (my figure 17), *M. microcyanthus* and *M. squarrosa*. The effects of stimulation are very similar in these species and seem to be characteristic of the genus as a whole.

FIGURE 17. *Acropora* sp. Part of an expanded colony of an unidentified species common at Ghardaqa. Characteristically one of the tentacles, that nearest to the apex, is longer than the rest.

The tentacles react individually to gentle touches with a seeker, which eventually drive a polyp to retract completely without any effect on the surrounding polyps. However, if a slight prick is made with a needle a wave consisting of a quick jerk of retraction of each polyp spreads rapidly over the stimulated twig of the colony. Sometimes a variable number (say three to six) of similar waves then spread further over the colony at intervals of 1 to 2/s. Each polyp gives a symmetrical jerk of column and tentacles.

This simultaneous protective response of many hundreds of polyps is produced by a *single* electrical shock above threshold applied anywhere on the colony surface. Herein lies a great difference between *Acropora* and other perforate corals on the one hand and the Actiniaria, Astraeidae and Fungidae on the other hand. A second shock initiates a similar wave of retraction over the colony. The extent of the spread of the wave rapidly increases at each shock, and a colony 50 cm across would respond everywhere at the third or fourth stimulus. A second response following the first within an interval of 5 s produces a response greater than normal. As followed by eye the velocity seems relatively slow for a giant fibre system and appears subjectively to be about 2 cm/s. In large colonies, observed by diving, contractions were observed a metre or so from a point where the skeleton was damaged.

Goniopora planulata Ehrb.

The polyps are expanded in full daylight. They are very regular, as in figure 18*a*, and spontaneous movements are rare. A tentacle that is touched with a seeker bends towards the mouth; neighbouring tentacles are not affected. With continued stimulation the column retracts smoothly and symmetrically into its tube, as in the feeding reaction described below. The tentacles are not greatly contracted lengthwise but remain as projecting stumps when the column has disappeared.

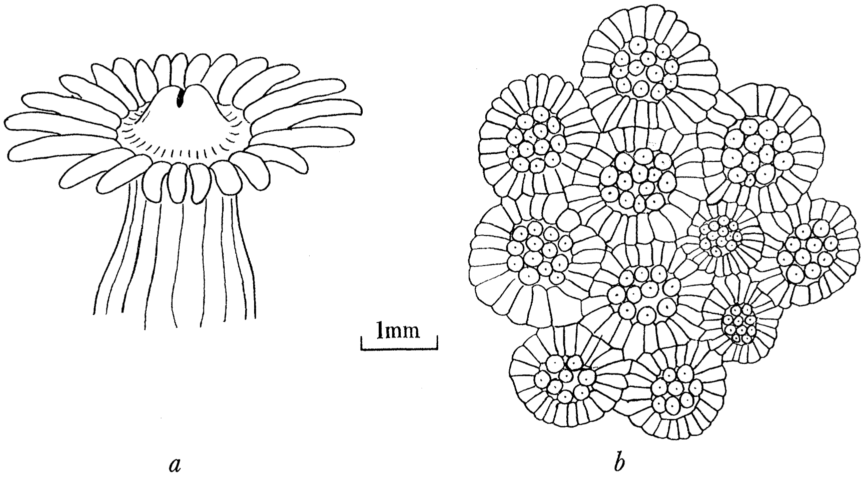

FIGURE 18. *Goniopora planulata*. *a*, a single expanded polyp. *b*, a group of partially retracted polyps seen from above.

When a particle of crab meat is allowed to fall on the tentacles or disk it is enclosed by the tentacles, which all bend inwards, and at the same time the column retracts slowly into the corallite. In contrast a single electrical shock above threshold, applied on the surface of the disk or column, immediately produces a symmetrical rapid *jerk* of the polyp to about half its original length and a shortening of the tentacles. It is impossible to produce an asymmetrical response. Neighbouring polyps are not usually affected. A second shock after 2 s interval produces a partial retraction of six or so neighbouring polyps, again as a definite jerk. With shorter intervals the response is increasingly strong, but it appeared that the number of affected polyps was not greater. After six shocks, at intervals of 1 s, about twenty polyps are three-quarters contracted and as many more on the periphery of the area are contracted to a lesser extent. With continued stimuli at 1/s it is impossible to drive more than 100 to 200 polyps to retract. By switching the stimuli to a second electrode close to the first it is shown that polarization of the electrode could not account for the failure of the response to spread. The result is similar when an expanded polyp is suddenly cut off; only a small area is affected. There is apparently an accommodation to the stimulus, or a limitation of the conducting system which will be discussed later. Besides this localization, the columnar arrangement of the skeleton also divides the colony into units between which there is no transmission of stimuli. The relation between the number of stimuli and the number of polyps affected is shown in figure 19*b*.

The response to a single shock on the surface of the corallite depends on the position of the electrode relative to the surrounding polyps, but, keeping this constant, the number of polyps affected increases to a maximum with increasing strength of the shock (figure 20). Experimentally the shocks were applied with various strengths in random order and with long intervals between them to avoid facilitation effects. The dependence of the extent of spread on the strength of the stimulus is an important point to be treated in the discussion.

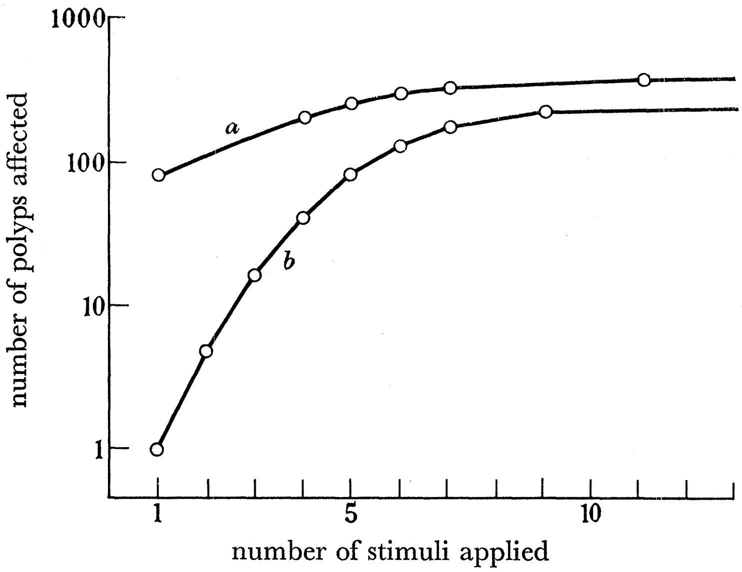

FIGURE 19. (*a*) *Porites* and (*b*) *Goniopora*. The relation between the number of stimuli and the number of polyps affected at a stimulation frequency of 1/s. Curves of this kind with decreasing slope and a maximum spread of excitation were characteristic of perforate corals except *Acropora*.

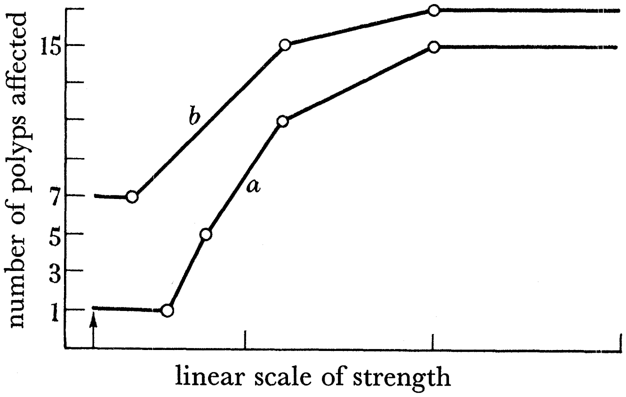

FIGURE 20. *Goniopora*. The relation between the strength of the stimulus and the number of polyps affected (*a*) by the first and (*b*) by the second shock, interval 1 s. Arrow shows threshold.

Porites

Three species of *Porites* were plentiful. They are the black columnar *P. columnaris* Klz., purple *P. lutea* M.E. & H., and buff *P. solida* Forsk. All react similarly unless the contrary is mentioned in the text.

By very gentle touch with a bristle it is possible to make one polyp contract without affecting its neighbours. However, a single electrical shock produces an immediate partial retraction over an area of 2 × 2 cm. This involves 200 to 300 polyps in what appears to be the contraction due to the spread of a single impulse. The number of polyps affected depends to some extent on the strength of the condenser discharge, as in *Goniopora*. With shocks just at threshold a much smaller response of twenty to thirty polyps could be obtained, as illustrated in the centre portion of figure 21.

Successive shocks at 1/s produce at first a progressive spread of the area of retraction but with decreasing effect (figure 19*a*). In *Porites lutea* the further spread at the second and third shocks is only about 3 mm, and more shocks at 1/s produce no further spread. In *P. solida* a spread to an area 4 × 4 cm is found after six shocks at 1/s, and additional shocks do not spread much further. A definite jerk of successive polyps spreads out as a wave from the electrode at each shock. Sometimes there are extra jerks, interpreted as some kind of after-discharge.

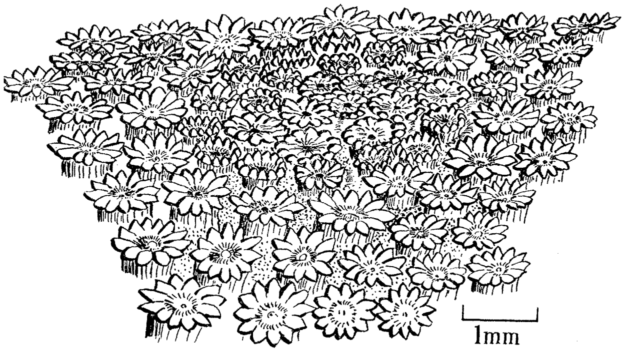

FIGURE 21. *Porites solida*. A group of expanded polyps to show the form of the colony. A single shock produces a partial retraction of a group of polyps as described in the text. The effect is shown in the centre of the picture.

An important point is that following a single shock the polyps near to the electrode retract more than those farther from it, a feature also observed in *Goniopora*. The consequences of this observation and a suggested explanation as to why the excitation from the first shock spreads so far and no farther will be found in the discussion.

Other perforate corals

I found that *Montipora verrucosa* Lam. and *M. stilosa* Ehrb. were difficult to observe on account of the small size of the polyps and their great sensitivity to light. *M. rus* Forsk. was more convenient. In each of these species a single electrical shock produces a wave of polyp retraction as in *Porites*, and this spreads over 2 to 3 cm^2. The same result applies to *Pocillopora favosa* Ehrb. and *Stylophora pistillata* (Esper.).

DISCUSSION

The behaviour of individual polyps

The individual polyps of all the species here studied have available a conduction system which co-ordinates their retraction by the endodermal muscles of the mesenteries. It may be inferred from the characteristic symmetry of the protective withdrawal on electrical stimulation that this system acts in a through-conducting manner, effectively as a single nerve. This physiological property is found to be more widespread than was formerly thought and polyps which do not respond symmetrically, for example, *Anemonia* (Pantin 1935*b*) are exceptional. In all corals studied except the perforate Madreporaria this system produces no contraction at the first electrical shock though it is everywhere active, as shown by the critical experiment of placing the second shock at a point distant from the first. The lack of response to the first shock makes it possible to determine the refractory period, which demonstrates that the conducting system behaves like an ordinary nerve with all-or-nothing properties and a single impulse at each electrical shock. These characteristics were thoroughly worked out for *Calliactis* by Pantin (1935*a*, *b*, *c*, *d*), and all I can add is the generalization to the polyps of the groups newly studied here. The protective retraction follows damage or electrical stimulation; the stimulus of food or touch differentiates between it and another series of reactions, which are localized feeding responses of great variety.

The feeding responses are slower and more continuous than the jerk of retraction, and the nature of the response is closely correlated with the form of each species. The responses are principally of the disk and tentacles, and are often associated with ectodermal muscles and possibly with parietal muscles where these occur. There is virtually no critical work on the nature of the transmission of the excitation in reactions of this kind in any coelenterate because of the difficulty of mechanically recording useful data, the impossibility of demonstrating a refractory period, and the inadequacy of the present histological data. This means that it cannot be shown physiologically that the nerves and the muscles are distinct systems or, except by analogy, that either is responsible for any of the conduction.

The only available physiological data for the analysis of such local responses refer to the disk of *Calliactis*, where Pantin (1935*a*) found that the strength of electrical shocks was of little importance but that with increase of the number and frequency of shocks the excitation spread farther and became more complex. Ten or fifteen stimuli were required before a conducting pathway was established from a tentacle tip to the sphincter. These observations, and, by extension, the apparently decremental conduction in all local responses, were interpreted as being entirely due to interneural facilitation, in which each impulse paves the way for a further spread of later impulses and in which a series of separate units becomes for a time a continuous pathway. In observations of the responses of individual polyps of corals I did not notice any features which would extend these conclusions. It can be seen that they apply in a qualitative way to the feeding reactions, particularly in the progressive spread round the disk, as, for example, in *Acabaria* (figure 1*b*), *Palythoa* (figure 6*c*) and *Fungia* (figure 13). However, before applying the concept of interneural facilitation to the transmission *between* polyps I would like to examine the quantitative implications of the model that is assumed.

The first model; interneural facilitation in a two-dimensional net

The observation that the stronger is the mechanical stimulation the greater is the spread of excitation was first satisfactorily explained without a violation of the all-or-nothing principle (as applied to individual neurones) by the concept of interneural facilitation (Pantin 1935*a*). Certain definite assumptions were made. These will now be expressed in general terms independent of any histological names such as 'cell' or 'synapse'. (*a*) There is a set of units each of which forms a number of connexions with its neighbours. (Originally the units were nerve cells; the connexions were synapses.) (*b*) The whole interconnected set forms a mesh which can be represented by a diagram such as figure 22, where in this particular example each unit has six connexions with its neighbours. Much of the explanatory value depends upon this assumption, which corresponds with the histological picture of an actual network of axons. (*c*) The connexions may be either conducting (*C*) or non-conducting (*NC*) at the instant when an impulse arrives. (*d*) Impulses are all-or-nothing. (*e*) In addition, we require an assumption which takes account of the progressive spread of excitation in nerve nets following successive stimuli. The following is the simplest: when an impulse arrives at an *NC* connexion it does not pass but the connexion becomes *C* for later impulses which may arrive within a specified time.

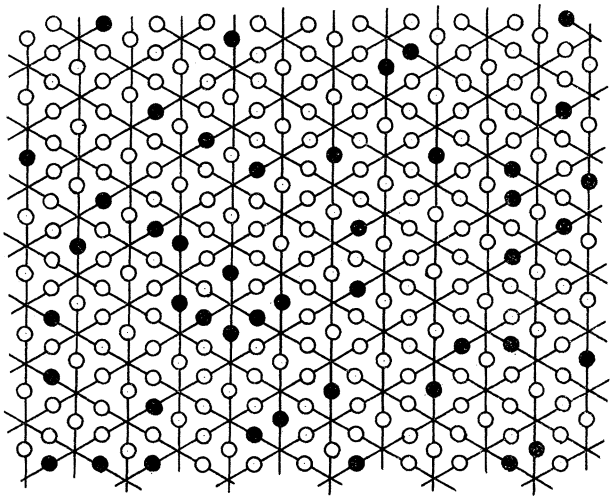

FIGURE 22. Part of an extended lattice of a model of a nerve net, as described in the text. The open circles represent connexions which are non-conducting and the black circles indicate conducting connexions. In this example the units are hexapolar, and about one-eighth of the connexions are conducting.

If all the connexions are initially *NC* then the area over which the first shock spreads, or the increment at each successive shock, can be at most the area covered by a single unit, and must be less than this if there is either overlap of units or uncertainty that a connexion becomes conducting whenever an impulse reaches it. This objection to the original theory of interneural facilitation as Pantin first propounded it may be overcome by supposing that (*f*) a proportion of the connexions between units are initially in the *C* condition at any instant.

An actual model which embodies these essentials has been constructed on a wooden board with holes, which bear index numbers, bored at the connexions. The *C* or *NC* character of connexions is indicated by pegs in the holes. By manipulation of this model it is possible to demonstrate the effect of changing various parameters of the system. Another assumption (*g*) is that connexions are independent of each other, which is another way of saying that *C* connexions are initially randomly distributed. This condition is easily fulfilled by reading from a table of random numbers the index numbers of those connexions which are to be fixed as conducting, until a desired percentage of *C* junctions is obtained.

With this arrangement the properties of a mesh with tripolar units and one with hexapolar units were examined for various percentages of conducting connexions. The analogy of applying a stimulus to a nerve net is an 'operation' on the model, where one particular unit is chosen. The total number of units connected to the chosen unit by *C* connexions is then counted, no matter how devious the pathways which can thus be followed. Then pegs of a different colour are put into the *NC* connexions which happened to be at the farthest limits of the pathways of the first operation and which have thereby been converted to *C* connexions according to assumption (*e*) of the initial premises. A second count is then made, as the second operation. This can be repeated for a third operation, by analogy with a third stimulus, but in practice two operations are sufficient to give the information required. The above procedure is repeated for every unit on the board, for any point is equivalent to any other, until a representative distribution of results accumulates. In figures 23, 24 and 25 are shown respectively the distributions of the number of units which respond to the first operation, to the second operation, and the ratio of these two numbers for the two operations on each unit. Each histogram is derived from 800 first and 800 second operations on the model, which readily provides more results than experiments with the animals themselves.

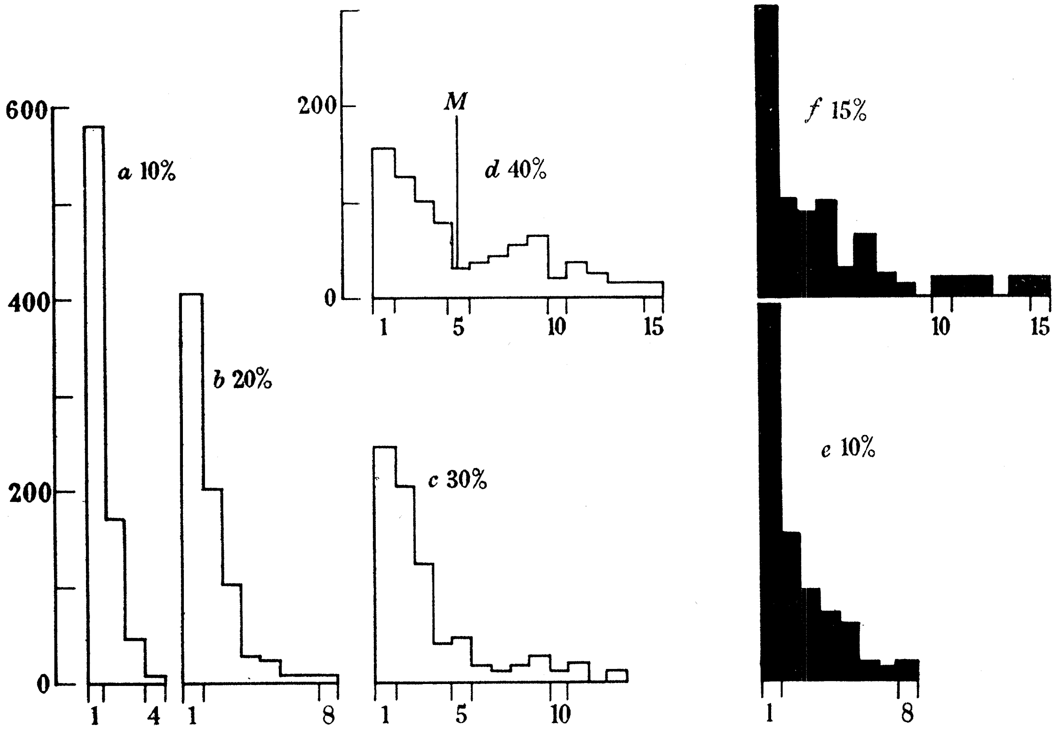

FIGURE 23. Histograms which show the distribution of the distance of spread of the first stimulus in experiments carried out on a model such as that shown in figure 22. Tripolar units with (*a*) 10 %, (*b*) 20 %, (*c*) 30 %, (*d*) 40 % of the connexions conducting; hexapolar units with (*e*) 10 % and (*f*) 15 % of the connexions conducting. These histograms show the number of units affected at the *first* operation (corresponding with the number of nerve cells fired by the first shock). Each histogram represents 800 experiments. Ordinates, frequency; abscissae, area of spread.

The model shows to a certain extent the right properties. The ratios in figure 25 show the extent of the facilitation at the second operation; in fact, this result is presupposed by the original assumption (*e*). As shown in figure 23 the number of tripolar units affected by the first operation increases with increasing percentage of *C* connexions. Through-conduction

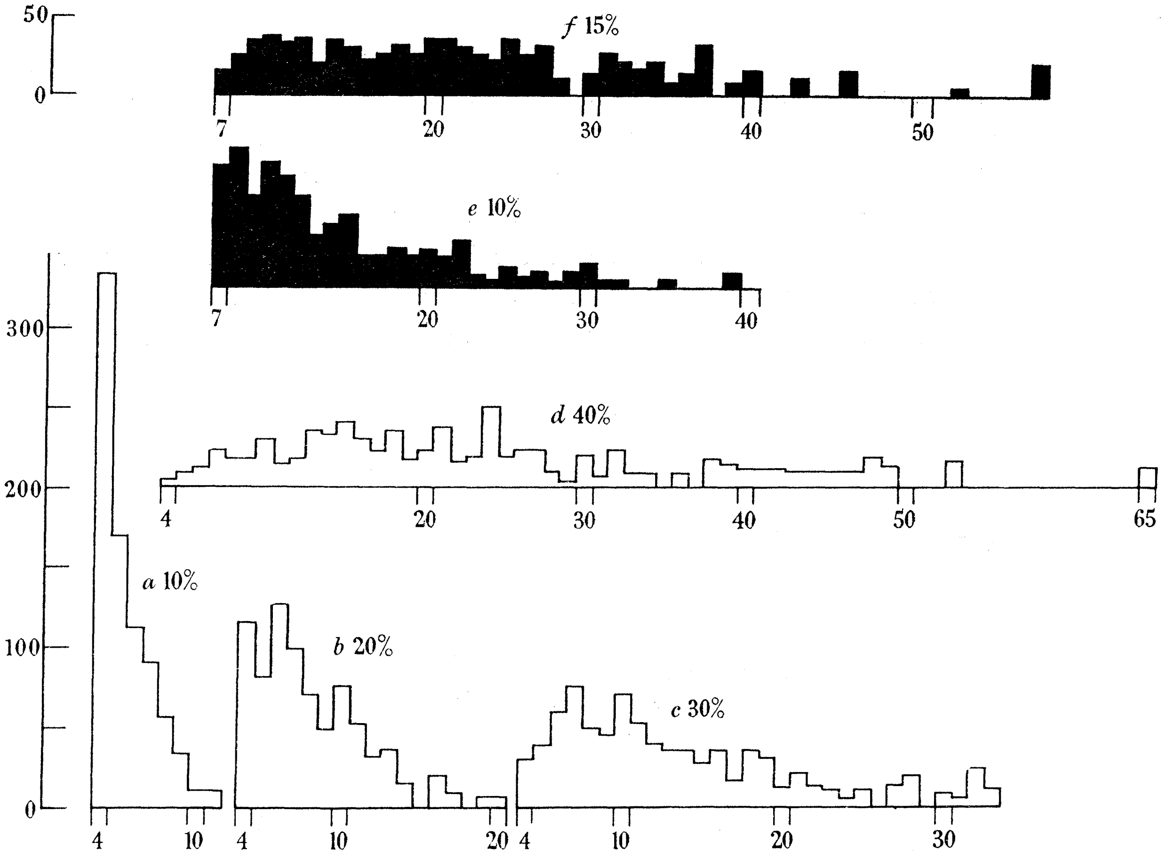

FIGURE 24. The number of units affected at the *second* operation. Subscripts are exactly as in figure 23. Ordinates, frequency; abscissae, area of spread.

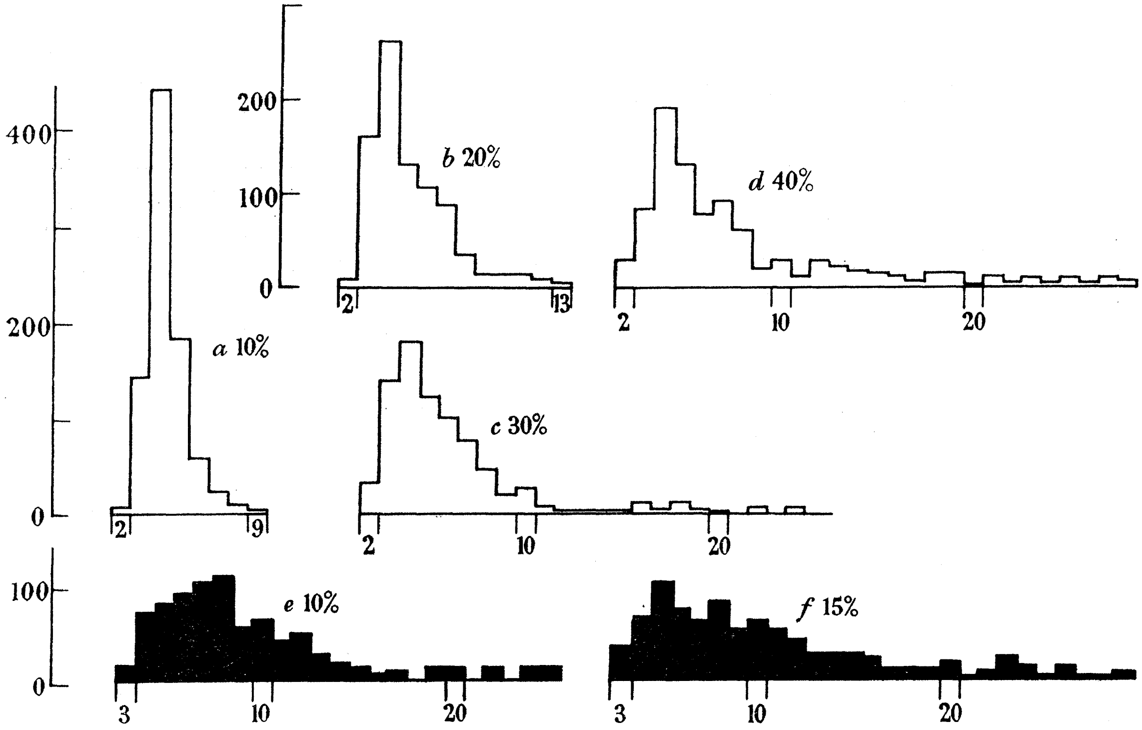

FIGURE 25. The ratios between the number of units affected at the second operation and the number affected at the first. Subscripts as in figure 23. Ordinates, frequency; abscissae, ratio of area of spread at second to area of spread at first operation.

(but not ubiquitous-conduction) begins to appear at about 50 % *C* connexions with tripolar units, and at about 20 % *C* connexions with hexapolar units. This alone is a result of interest. However, the important feature of the results is their high variability when there are sufficient *C* connexions to ensure that at the first operation the spread goes beyond the unit 'stimulated'. As shown by comparison of figure 24 with figure 23, the second operation produces a much more variable spread than the first. With tripolar units and 40 % *C* connexions, which ensures an average spread of 5·3 units at the first operation (*M* in figure 23 *d*), the spread at the second operation ranges from 4 to 65 units with no particular peak (figure 24 *d*). A consistent measurable property cannot be found by use of the ratios shown in figure 25, and again the ratio is not a useful measure of the percentage of *C* connexions because it depends less on the condition of the junctions than on the number of connexions per unit and on the overlap of the neurones in actual nerve nets.

The above results apply equally well to hexapolar units except that here a smaller percentage of *C* connexions gives any particular result and through-conduction appears at about 20 % *C* connexions.

There is no reason to think that the characteristic high variability of this model may be reduced by choice of a particular pattern, the introduction of overlap of units, or change in the number of connexions per unit. In fact, similar results follow from a consideration of randomly distributed pathway elements of any kind, for example, in the maximum length of perambulation available to an insect with a path confined to straw scattered thinly but haphazardly on the ground. The great variability of the number of the affected units, particularly in the second and succeeding operations, can be readily avoided by the introduction of an extra assumption. For example, there could be defined a model such that a unit may change its condition as a whole so that all its connexions become conducting, but also that at the same time neighbouring units are then incapable of this change except following an impulse. This is an artificial device which would prevent the formation of long devious pathways by the juxtaposition of randomly distributed *C* connexions. But such an arrangement, in which a unit with conducting connexions might inhibit surrounding units, implies a physiological inhibition for which there is no separate evidence. It is of no value to fabricate an explanation by invention of further complexities of this kind. The first model shows that there are only two conditions under which the extent of the spread at each operation is not very variable; they are the through-conducting (all *C*) and its opposite (all *NC*).

At this stage it must be made clear that the units of the model may represent either neurones or groups of neurones which act together, i.e. are through-conducting within each group. For example, units may represent polyps, or tentacles. There is a temptation to equate *connexions* of the hypothetical model with physiologically observed *junctions* and again with histologically observed *synapses*, but this is not required in the present discussion, and to be valid these must be proved separately. The model is only a physical representation of the assumptions and is subject to all the dangers of misplaced concreteness in its parts. It is a straightforward interpretation of the current theory of interneural facilitation, which is derived from Pantin (1935 *a*) and frequently expressed (e.g. Ramsay 1952, p. 105). Bearing in mind how the assumptions work out in practice we are now in a position to discuss the different degrees of co-ordination between the polyps of the various groups of corals.

Discussion of the observed transmission of excitation between polyps

Two of the types of transmission between polyps can be dismissed immediately. First there are those examples with little or no co-ordination, *Acabaria* as an example of a gorgonid, and *Lobophyllia* of a madreporarian. Secondly, there are the forms which have a through-conducting system between large numbers of polyps; for example, the alcyonarian *Tubipora*, the astraeids *Favia* and *Coelaria* and the perforate coral *Acropora*. Here, if the through-conducting pathway is not immediately evident over the whole colony there is no consistency about the extent of the spread of excitation at the first applied shock or the increment of spread at successive shocks. An occasional accumulation of *NC* junctions, which are observed to break down easily to give through-conducting properties, would explain the failure to conduct over the whole colony. It seems that effectively there is continuity between neighbouring mesenteric through-conducting units.

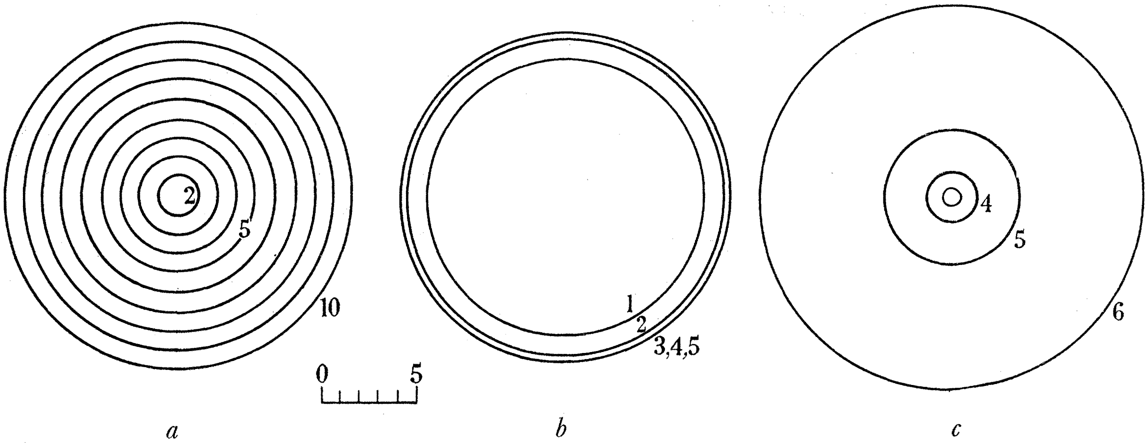

FIGURE 26. A representation of the spread of excitation across the colonies of (*a*) *Palythoa* and *Galaxea*, (*b*) *Porites*, and (*c*) *Sarcophyton* following various numbers of shocks. Apart from the through-conducting systems, these are the principal types of the spread of excitation so far observed in corals. The scale shows the probable size of conducting units.

There are two examples, *Palythoa* and *Galaxea*, in which the units are the polyps, each with its own through-conducting mesenteric system. Between polyps the transmission behaves as if there are everywhere *NC* junctions, which progressively become *C* junctions as a succession of impulses spreads across the colony. The leading impulse apparently disappears at each *NC* junction reached and paves the way for its successor to pass to the next *NC* junction. This is the model originally postulated as interneural facilitation, but with initially no *C* connexions between units. The model fits the facts because the distance of advance of successive impulses is consistent with the probable size of units. The result may be summarized by the diagram (figure 26*a*), in which circles indicate the limits of spread of waves from successive shocks.

We have still to account for the behaviour of *Porites* and *Sarcophyton*, which are represented in figure 26*b* and 26*c* drawn on the same scale relative to the expected size of the conducting unit. We expect the area covered by the processes of a neurone to be of the same order as the diameter of a polyp, certainly not much more than this, though histological data is lacking. In *Porites* the excitation from the first shock spreads equally in all directions across a distance at least ten times the diameter of the polyps. The large size and at the same time the regularity of the affected area do not agree with the theoretical results shown in figure 23. At the second and later shocks the total spread is not much larger than at the first shock. The model predicts a much larger spread at the second shock. Two further observations, the smaller response at the edges of the area and the effect of stimulus strength, cannot be explained by the model. It is of no value to return to the older theory that the excitation decreases in strength as it travels from the point of stimulation. This is Bozler's 'dekrement' which is contrary to the all-or-nothing principle for single impulses (see introduction to Pantin 1935 *a*). The responses to a single shock have an appearance which suggests that the excitation is one impulse, not several. The relatively small increment of spread at the second and later shocks cannot be attributed to a partial loss of sensitivity because the stimulated neurone (assuming the first model) must be either excited or not.

In *Sarcophyton* (figure 26 *c*) there is normal inter-unit (possibly interneural) facilitation at first, but after a few shocks the increments of spread at successive shocks increase more and more. On the other hand, with stimuli at 15 s intervals the transmission appears to be similar to that in *Porites*. Stimuli at 1/s finally initiate a wave of excitation which spreads everywhere in the colony. The first model never behaved like this.

The second model; a population of nerve cells, a proportion of which is active at each wave of excitation

The variability of the first model arises from the assumption that only one unit is acted on by the stimulus, and it is a matter of chance how many other units are connected to it. In a new model we must therefore avoid the concept that the length of available pathways depends upon the juxtaposition of a *small* number of randomly distributed C connexions. Moreover, a great many nerve cells are stimulated together in actual experiments with relatively large electrodes. We may therefore consider the proposition that the nerve net is a population of nerve cells, and what we have been calling 'excitation' is an impulse or series of impulses in a *proportion* only of the cells in any small region.

Consider a mesh of units as before, with the property that an impulse in any unit has the probability P of crossing over to a neighbouring unit. With P less than unity the number of active units will die away exponentially from the centre of origin. If the initial density of active cells is d_0, the density d_1 after the first connexion will be $d_1 = d_0 P$, and after the nth connexion will be $d_n = d_0 (P)^n$. Figure 27 *a* shows these exponential curves for $P = 0{\cdot}9$ and various values of d_0. Given a critical density of active cells d_c which is just sufficient to produce a visible response, then the extent of the spread relative to the size of units is given by the distances OP, OQ, etc. Sufficiently large numbers of units are active to ensure consistent results; a decrement is possible without violation of the all-or-nothing action of individual units. At a second stimulus the same process can happen again; but it is to be expected that a second stimulus will activate a larger initial density of active cells, and P may have changed within the area of spread of the first stimulus. We have therefore two additional relations, of d_0 and of P with frequency, with which to interpret facilitation effects. The usual interpretation is that P increases for a short time after a stimulus has passed, i.e. that junctions tend to remain open. This would produce a progressive spread at successive stimuli as in *Palythoa* and *Galaxea*, and d_0 may well remain constant. If we consider the responses of *Porites* and *Goniopora* the features which have been difficult to interpret are (*a*) the large regular spread at the first shock, (*b*) the dependence of the spread on the strength of the shock at low intensity, (*c*) the apparently decremental fall-off of the response at the margin of the area of spread and (*d*) the small increment of spread at successive shocks. Each of these observations is readily explained by the new theory as (*a*) the regularity produced by large numbers of active neurones; (*b*) and possibly (*d*) the effect of d_0 on the distance of spread OP, OQ, etc., in figure 27*a*; and (*c*) the smaller contraction elicited by a smaller proportion of active nerve cells. The possibility of extending such arguments to nerve nets other than the co-ordinating system of coral colonies is already apparent. But figure 27*a* contains nothing but exponential decay of 'the strength of the excitation' with distance from the point of stimulation. In *Sarcophyton* there seems to be an interaction of the excitation with itself; the greater the local response, the greater is the tendency for the transmission to be self-sustaining, until eventually a wave spreads across the colony as illustrated in figure 8. We can represent this as $d_1 = d_0\ (P + \alpha d_0)$ instead of $d_1 = d_0\ (P)$, so that the probability of an impulse crossing a connexion depends on the existing density of active units. This gives a Bernoulli equation which is solved and in part plotted numerically in figure 27*b* with $P = 0{\cdot}9$ and $\alpha = 0{\cdot}001$. There is a fall-off as before for $d_0 < 100$, but there is a wave of excitation of all units for $d_0 > 100$. Successive stimuli might be considered to produce increasing values of d_0. The required threshold is reached at the point when there is

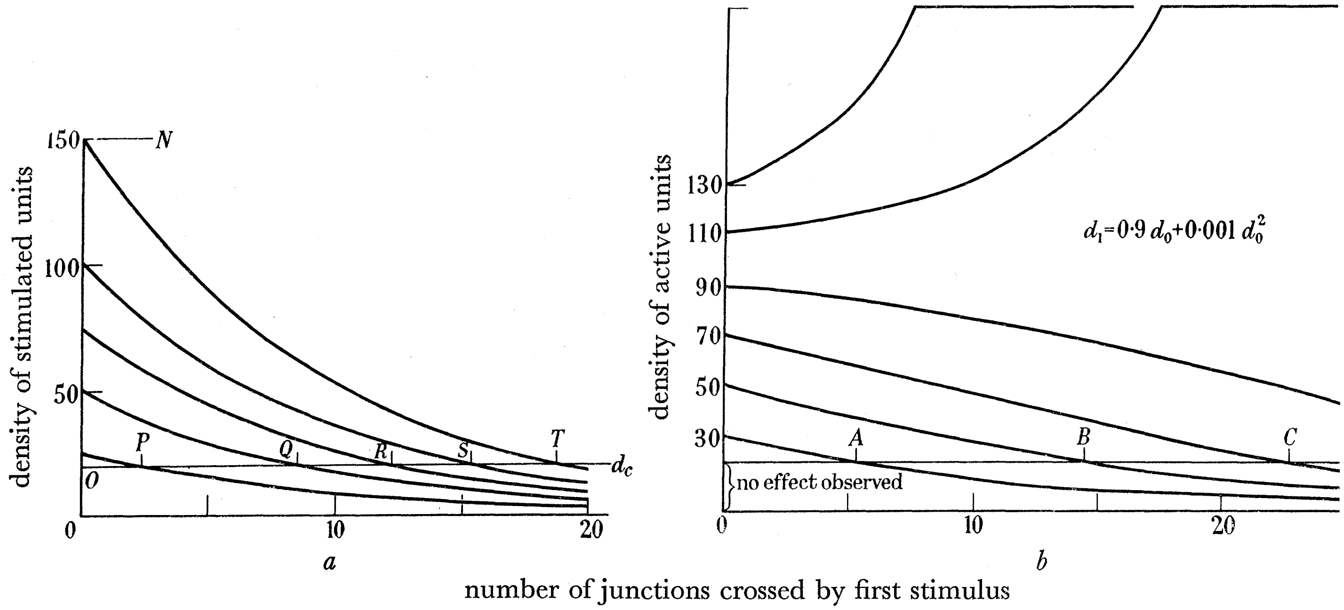

FIGURE 27. (*a*) A representation of the spread of excitation from a single stimulus as deduced from the postulates of the second model described in the text, without interaction between units. When a greater density of units are stimulated a greater number of junctions are crossed and the excitation spreads farther as shown by the points *P*, *Q*, *R*, *S*, *T*. The line d_c represents the lower limit of density of stimulated units below which there is no visible response. (*b*) As for 27*a* except that there is now some interaction between active units, the result of which is to produce a propagated wave over the whole colony when more than a critical number (in this case 100 units) is stimulated.

sufficient activity for it to be self-maintaining. This seems to represent what happens in *Sarcophyton*; also the concept of some interaction between nerve cells in a nerve net is of wider application than this particular example. The extra term that produces relatively greater interaction at greater values of d_0 is in fact a mathematical representation of spatial summation, long known from other nervous systems. With large numbers of cells it is possible to have very little summation (i.e. very small values of α) to produce the required effects.

An objection might be raised that this model is made so versatile by the possible choice of parameters that it can explain anything and therefore has no value. However, this is the simplest model that assumes a population of nerve cells, not all of which need be active, and with spatial summation between cells added in one special case, for *Sarcophyton*. It assumes that the probability P of transmission between units has some meaning in a real nerve net. The results do not depend on the number of connexions per unit, nor on the arrangement of the connexions, for these factors are contained in the probability P. Through-conducting pathways are then of two kinds: (*a*) those where continuity can depend on a single fibre and each fibre always passes excitation to *several* others (this is equivalent to putting P greater than unity), (*b*) those with a higher value of the threshold density of active cells required to initiate a wave. Experimentally these could be distinguished by the use of bridges with few fibres. For example, the *Aurellia* giant fibre net is of the first category (Horridge 1954).

The problems set by colonial co-ordination in *Sarcophyton*, *Goniopora* and *Porites* have led to a concept of interneural facilitation that may be useful in the interpretation of the activity of all nerve nets, for all that has been done is (*a*) to see how a few basic assumptions work out in practice and (*b*) to find a correspondence between the behaviour which such a set of postulates predicts and the observations on actual animals. The particular theory chosen has been of value to explain the generalizations derived from physiological experiments on many different species. This is a zoological method. The theory is also chosen to be compatible with the histological background, which is, however, inadequately known at present. The new theory is compatible with the ideas which led to the original formulation of the theory of interneural facilitation and also with the observations on the anemone tentacle reactions which supported that theory. At the same time new experiments are suggested; for example, the size of the stimulating electrode is now seen as a possible factor which can influence the distance of spread of the excitation. As yet there has been no direct test of the central hypothesis, that from the large number of nerve fibres which make up the net only a proportion may carry an impulse when a wave of excitation passes. This would require simultaneous observations of many fibres, intrinsically a difficult task. We are left, therefore, with the explanation in terms of the second model, which corresponds best with the observations. There remains the difficulty of all interpretation of this kind, that further indirect tests, however corroborative, may also agree with other models which the imagination has not yet produced.

CONCLUSION

The basis of the discussion has been that the several types of co-ordination between the polyps of corals can be reduced to variations on a common theme. The results are summarized in figure 28 where there are three types of curve: those with decreasing slope, those with increasing slope, and the straight lines, both those at the top of the diagram and that for *Palythoa*. These curves may be interpreted in terms of a new theory which considers a population of nerve cells, each one of which may pass an all-or-nothing excitation to its neighbours. The theory depends on the postulate that only a proportion of the nerve cells in any small region may carry an impulse when a wave of excitation passes. This has not been directly observed, but it provides a means of explaining new observations which are at variance with the existing theory of interneural facilitation. The new theory is an extension rather than a replacement of the earlier one which assumes that all cells are active when the nerve net is excited. The earlier assumption predicts an independence of the response from the strength of the stimulus, but fails to explain why the response spreads consistently so far and no farther, with a smaller response at the margins of the affected area. The new theory explains in addition the change in slope of the curved lines of figure 28. Consider first the curves with decreasing slope. Successive shocks serve to increase the density of active neurones near the stimulated point, and this pushes the excitation a little farther. The exploitation of new pathways by successive shocks (on the older theory of interneural facilitation) plays only a small part here since a maximum spread soon appears, however many shocks are applied. We may explain the curves of increasing slope by introducing a small amount of spatial summation between nerve cells such that the more cells are stimulated at any point the greater in proportion is the number of adjoining cells to which the excitation is passed. Eventually this leads to the formation of a wave of excitation in which most of the neurones of the colony are active.

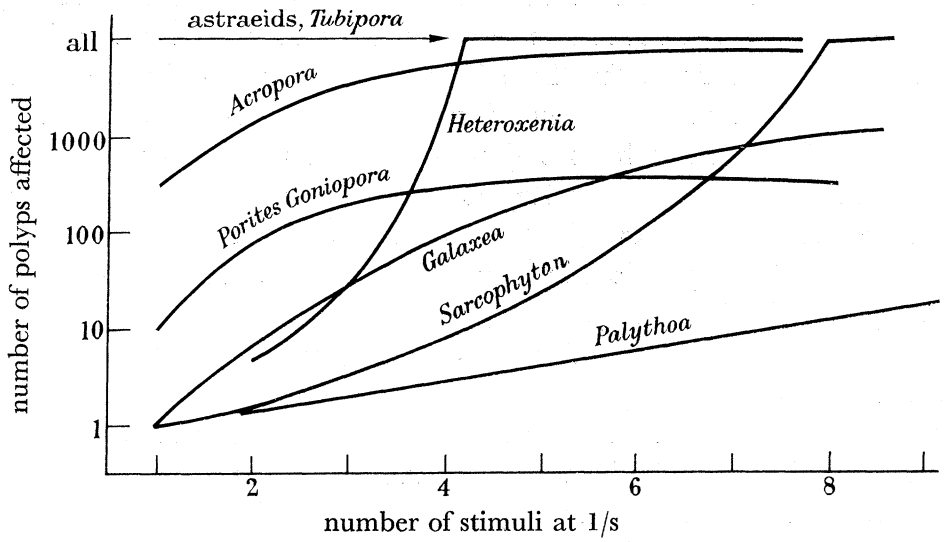

FIGURE 28. The relations between the number of stimuli at 1/s and the number of polyps affected for a variety of the corals discussed. There are three kinds of response: the ones in which the whole colony is active from the first stimulus, shown by a horizontal line at the top of the picture; the ones with an increasing slope such as *Heteroxenia* and *Sarcophyton* in which ultimately a wave spreads over the whole colony; and those with a decreasing slope in which the response spreads to a limited number of polyps no matter how many stimuli are given. Observations on *Heteroxenia* are published separately (Horridge 1956).

Individual examples of co-ordination in coelenterates may be explained by particular mechanisms, but the second theory here presented embraces both interneural facilitation, the older descriptions of decremental conduction, and through-conducting systems, together with the known conducting systems in *Sarcophyton* and perforate corals, which do not fit the other categories.

I should like to thank Professor H. A. F. Gohar for allowing me to work at Ghardaqa and the many people who were friendly to me there. Special thanks are due to the Anglo-Egyptian Oil Company and the Shell Company of Egypt for the varied assistance they rendered to me, and there is a personal debt of gratitude to Mr and Mrs MacGavin of Suez. This work was carried out during the tenure of a senior award from the Commissioners for the Exhibition of 1851; and I should like to thank the Royal Society for a grant towards expenses.

Postscript (*added in proof* 27 *February* 1957). A paper by Beurle (1956) has appeared in this journal since this manuscript went to press. To anyone who compares his figure 3 with my 27*b* it may be striking that he should be primarily interested in the cerebral cortex while I have been independently concerned with the most primitive nervous systems. Both Beurle and myself admit that our respective theories only show how a set of suppositions work out in practice. We differ in our treatment in that Beurle starts with more parameters with which to describe his nerve cells and he takes the analysis much further. On the other hand, the phenomena he sets out to explain are more complex. A model with a large number of random connexions between units may well be found to correspond to other examples of the collective activity of nerve cells.

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