# COORDINATION IN THE STARFISH



BY

W.illiam F.erguson HAMILTON 1893—

A Ph.D. Thesis

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## INTRODUCTION

Although the behavior and physiology of starfish and other echinoderms have been given the attention of many and eminent naturalists, it was hoped that an intensive study of the problem of coordination in the several species available would bring to light some data, that might prove of interest to the physiologist and general zoologist.

The work was commenced in the autumn of 1917, but in December was interrupted by fourteen month's service in the army. Between February 1919 and June 1920 I have spent most of my free time experimenting upon and observing the activities of starfish. It would be quite impossible to set down my data in full, following each experiment and observation out in detail, for reasons of space alone. My evidence, therefore, has undergone a rather severe selective process.

## ACKNOWLEDGEMENTS

I wish here to express my thanks to Professor S. J. Holmes under whose direction the following study has been made, for his careful criticism and his many helpful suggestions. I am greatly indebted to Professor W. K. Fisher, of the Hopkins Marine Station of Stanford University, for his courtesy in putting the facilities of his laboratory at my disposal, and for his help in collecting and keeping alive the material. He was also kind enough to determine the species I worked upon. I wish also to express my thanks to Professors S. S. Maxwell and T. C. Burnett, of the Physiology department of the University of California for their helpful advice.

To my wife, for her many cheerful sacrifices and her willing help in numerous ways, is due my fullest gratitude.

MATERIALS.

The following starfish were studied intensively:

Pisaster ochraceus (Brandt)

Pycnopodia helianthoides (Stimpson)

Asterina miniata (Brandt)

Supplementary observations were made on the following echinoderms:

Leptasterias equalis (Stimpson)

Pisaster brevispinus (Stimpson)

Evasterias troschelii (Stimpson)

Strongyocentrotus franciscamus (Agassiz)

Professor W. K. Fisher writes me as follows "Jennings (1917) worked on Asterias sertulifera Xantus. I have the actual specimen sent, for identification to the Museum of Comparative Zoology. Verrill calls the same species Orthasterias gonalena." Jennings uses the name Asterias forreri De Loriol.

So far as I am aware, the above seven species are the only Pacific coast starfish, whose physiology has been described.

PHYSIOLOGICAL STATES

Piaster ocraceus, was collected from the wharves in Oakland harbor for study in the zoological laboratory of the University of California. For study in the laboratory of the Hopkins Marine Station they were obtained from the surf beaten rocks in front of the building.

A remarkable difference was evident in the physiology

of the specimens taken from these two locations, which was not, so far as I was able to determine, due to the salinity of the water in the aquaria, its temperature, freshness, air content or the food needs of the animal.

*Pisaster* taken from the surf-beaten rocks were very inactive, would attach tightly for long periods of time to the substrate, and could not be excited to active locomotion by the most varied, persistent, or continued stimulation. The water in the aquaria was running freely and would keep these animals alive and other animals ( starfish, crabs, sea-urchins etc.,) alive and active indefinitely.

The specimens of *Pisaster ocraceus* taken from Oakland harbor presented, when fresh, activity of an almost opposite nature. It was quite as difficult to get them to stop crawling as it was to get those from the surf beaten rocks to start. In some specimens this state of extreme activity never appeared; but in the large majority it appeared when the animals were first put in the aquarium and, continued, interrupted by rest periods of greater or less extent, for from two hours to two months.

The only specimen from the surf-beaten rocks at Pacific Grove which showed this marked locomotor activity was one that had been in the quiet water of the aquarium for nearly three weeks. At the end of this period the animal forsook the tight clinging which had occupied it during its struggle to maintain a foot hold on the rocks and began active migration.

The specimens occurring on piles in the relatively quiet waters of Oakland harbor do not attach very tightly, though they can do so when disturbed and are not nearly so prone to attach when brought to the aquarium.

I am not inclined to attribute this behavior to "learning"

(see Sterne 1891) nor even to habit formation (Jennings 1907), but would explain it more simply as a very marked and striking example of "physiological inertia":(Jennings 1907) or the tendency to tontinue past responses in spite of present stimulations. We shall inquire further into the nature of this tendency. (see also Romanes & Ewart (1881), Preyer (1886), Mangold (1908b), Bohn (1908), Cowles (1911a), Holmes (1911), Cole (1913a).

To the two physiological states above noted, the one of extreme rigidity and attachment and the other of active locomotion with the arms more or less extended and flexible we may add a third state in which the arms are extended as in the locomotor state but the tube feet are not oriented in any particular direction as they are in the locomotor animal. The tube feet are more or less active and not tightly attached.

Animals in these three states will be referred to as (1) locomotor or crawling starfish, (2) rigid starfish and (3) active but unoriented, or resting starfish respectively. In these different states the animal's behavior is wholly different.

Pycnopodia helianthoides the large 20 rayed "sun star" present these same physiological states in quite as marked a manner as Pisaster. I have never observed Pycnopodia to assume the rigid or attached state when on a horizontal substrate. It will attach quite readily to a vertical substrate, and with such tenacity that it is very difficult to remove it, but on a horizontal substrate I have observed it (see Stevens 1902) nor even to habit formation (Jennings 1907), but would explain it more simply as a very marked and striking example of "physiological inertia": (Jennings 1907) or the tendency to continue past responses in spite of present stimulations. We shall inquire further into the nature of this tendency. (see also Romanes & Ewart (1881), Preyer (1886), Mangold (1908b), Bohn (1908), Cowles (1911a), Holmes (1911), Cole (1913a).

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In Asterina the physiological states are not well differentiated. The animal does not attach tightly though it does become rather rigid and inactive. The locomotor state is clearly marked, although in the unoriented state one often sees the animal make lurches, as if to crawl in this and then in that direction without actually doing so.

The other starfish observed seem to present different physiological states more or less analogous to those described for Pisaster.

In the following pages we shall discuss the responses of the tube feet as individual organs, their coordination among themselves, and the relation of these movements to the coordination of locomotion and righting.

RESPONSES OF A SINGLE TUBE FOOT

The tube foot of a normal starfish may exhibit the following responses, which vary, as we shall see, with the physiological state of the animal: (1) extension, (2) attaching, (3) withdrawal, (4) step reflex.

EXTENSION

Conditions of extension

Extension of the tube feet is best seen in the active starfish upon the absence of those stimulations which normally cause a withdrawal of the tube foot or complicate its extension by inducing the activities of attaching or "stepping."

To study the factors which govern simple extension of the tube feet it is necessary then to invert the animal on its aboral side, or better yet to suspend it freely in the water. Thus are avoided the disturbance of contact stimulation.

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Direction of extension

The extension is conditioned in direction by the locomotor activity of the animal as a whole. If the starfish is migrating in the direction of a certain arm, for instance, the tube feet will, in the absence of contact stimulation extend themselves in this direction, and remain so extended until stimulated either to retract or execute the step reflex.

In the stationary, non-rigid starfish the tube feet of the outer part of the ray are, in the absence of contact simulation, extended more or less toward the tip of the ray and ~~on~~ moving ("feeling") about in that direction. This of course is not constant and is most noticeable in the most active specimens.

Starfish that are inactive or in the rigid state do not extend the tube feet as much as do individuals of the active non-locomotor type. The most noticeable difference between the behavior of the tube feet of such a starfish and those of a normally active one is that the former are not directed ~~out~~ away from the tips of the rays. They may be waving about approximately at right angles to the ray or even directed somewhat toward the center.

Mechanism

The mechanism of extension, first described by Reamur (1710) in a very interesting paper is well known. It involves a contraction of the ambulacral ampulla and a relaxation of the longitudinal musculature of the tube foot. To ascertain the dependence of this relaxation of the longitudinal musculature on the radial nervous system, tube feet were cut off and tied on to the end of a capillary glass tube. This was connected with a column of sea-water arranged so that the pressure could be

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Active tube foot preparations were allowed to extend and assume their normal curvature toward the pseudohaemal canal, and then were bent slowly and gently in some other direction. They showed a tendency to remain bent in that direction and then slowly to bend back to the original curvature. An anaesthetized or a dead tube foot does not show this behavior. It is hence physiological in its nature and is perhaps analagous to the behavior of a sea-urchin's spine when bent over to one side (Von Uexküll 1900 ).

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Attaching

Attaching is conditioned by the physiological state of the organism. The tube feet of Pisaster in ordinary locomotion do not attach very strongly. When in the rigid appressed state, however, they are so tightly adherent that many may be pulled off before the animal can be removed from the substrate.

Strength of attachment.

Mr. Weymouth of the physiological department of Stanford University informs me that he has released the tube feet of such a starfish one by one with a needle until there were just enough tube feet adhering to suspend the animal from the lower surface of a glass plate. The estimated area of the disks of these tube feet multiplied by atmospheric pressure was approximately equal to the weight of the starfish thus showing that these organs are mechanically quite efficient.

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Tube foot preparations were made as above from actively attaching starfish, great care being exercised to work quickly and gently. It was found upon placing such a tube foot against a substrate that in about five cases out of ten, it would attach and hold against considerable tension (in one case enough to tear off a part of the disk). This power of attaching was lost after a few trials.

Dependence of attaching reaction in isolated tube feet upon physiological state of organism.

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## Dependence of Attaching reaction in isolated tube feet upon physiological state of organism.

Tube foot preparations were also made from starfishes that were not attaching (in active locomotion, feeling about the surface film, etc.) These did not attach.

The interpretation of this phenomenon is rather difficult. It is well known that when an attached starfish is pulled off from its substrate, many of the tube feet will be torn off and may remain attached to the substrate for some time. The experiment shows further that such a tube foot may reattach even tho it be unconnected with the radial nervous system (see also Botazzi 1898 and Russo 1913).

It is well known, also, that some times a starfish is very prone to attach its tube feet tightly to the substrate while at other times the animal's energy is taken up with locomotion or some other activity that does not entail tight attachment of the tube feet (Jennings 1907). The experiment shows also that there is a difference in the behavior of the isolated tube feet which corresponds to the fluctuation of the attaching reaction of an animal from time to time.

According to Von Uexkull, the contraction of a muscle is due to "Tonus" which is metaphorically referred to as a fluid, that is carried to the muscle through the nerves. Furthermore (1903) by cutting the nerve which has supplied this tonus, the "fluid" may be entrapped in the muscle, and the muscle remain contracted. While this theory has not been very widely accepted, (Mangold 1909b) some of its aspects are partly congruent with the behavior of isolated tube feet.

Tube foot preparations, however, that are capable of attachment do not present any differences in appearance from those that are not capable of attachment. Thus they are not influenced by entrapped "tonus" in the sense of Von Uexkull because "tonus" elicits contraction or tension in the muscles it affects and the tube feet under observation did not seem to differ in this respect from tube feet which would not attach to a substrate. In fact they differed from tube feet taken from a starfish in active locomotion only in being in such a state of physiological activity that the

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It would seem, then, from the difference in behavior of tube feet taken from animals in different physiological states that this state of specialized irritability is a condition of the ambulacral disk and while engendered, most probably, by influences proceeding from the radial nervous system, is not dependent upon that system for a rather limited continuance.

Attaching by only a part of the ambulacral disk.

The attaching reflex does not necessarily involve all of the ambulacral disk. The end of a small rod was placed on various parts of the lower surface of a large actively attaching pedicel. The part in contact with the end of the rod attached with great force, such that an attempt to withdraw the rod resulted in pulling a portion of the disk out of shape. A fine hook was laid flat against the disks

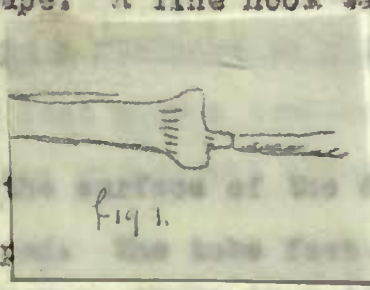

Fig 1.

of tube feet so that the surface of the disk in contact with the instrument was hook-shaped. The tube feet attached to the hook quite strongly. In fact, any part of various disks was found to attach even to the point of a needle, when this was applied gently enough. These experiments were repeated upon isolated tube foot preparations with the same result.

The disk as an attaching mechanism, then, does not act as a whole (Preyer 1886), but rather the incupping occurs toward the center of any properly stimulated area.

WITHDRAWAL

Releasing and withdrawal as a result of stimulation of side of column.

Release of attachment and withdrawal are two responses attaching reflex is the one that contact stimulation elicits.

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WITHDRAWAL.

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that are closely analagous. If a starfish is tightly attached to the side of the aquarium, to get it off without injury to the tube feet, one has but to stimulate the sides of the tube feet sharply with the edge of some flat instrument that will slip under the starfish. This stimulation causes the release of the stimulated tube feet and sometimes the release of neighboring tube feet.

If a starfish be inverted or suspended, when not exhibiting a locomotor tendency, and the side of an extended tube foot be touched even very lightly, there is an immediate collapse and withdrawal of the tube foot. Careful observation of the phenomenon leads one to think that it is a result, first of the relaxation of the ampulla and second of a contraction of the longitudinal musculature of the tube foot.

Withdrawal as a response to stimulation of the disk.

If the tube feet show a tendency neither to locomotion nor to attachment, this same withdrawal reaction follows the stimulation of the disk.

Usually, however, there is a tendency toward attachment which does not necessarily interfere with the presence of the withdrawing reaction. This conclusion was reached from a study of the reactions of tube feet to very light suspended objects. A small piece of thin celluloid, suspended by a thread, was brought in contact with extended (non-locomotor) tube feet. The first response, usually was found to be attachment. After this, depending on conditions which will be that are closely analagous. If a starfish is tightly attached to the side of the aquarium, to get it off without injury to the tube feet, one has but to stimulate the sides of the tube feet sharply with the edge of some flat instrument that will slip under the starfish. This stimulation causes the release of the stimulated tube feet and sometimes the release of neighboring tube feet.

If a starfish be inverted or suspended, when not exhibiting a locomotor tendency, and the side of an extended tube foot be touched even very lightly, there is an immediate collapse and withdrawal of the tube feet. Careful observation of the phenomenon leads one to think that it is a result, first of the relaxation of the ampulla and second of a contraction of the longitudinal musculature of the tube foot.

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Detaching and withdrawal of isolated tube feet.

An isolated tube foot preparation does not show typical withdrawal reactions, because of course, the reciprocal action of the ampulla is absent. Harsh stimulation of the column of the attached tube foot preparation was found to cause release. Shortening by a slow contraction of the longitudinal musculature was found to follow severe stimulation of any part of the tube foot, even against a strong water pressure.

Response to internal changes

Release and withdrawal ~~xx~~ of attached tube feet may occur as a response to a change of internal physiological conditions. Thus an animal all of whose feet were tightly attached, one minute, may the next minute be seen in active locomotion about the aquarium. The factors governing this response will be taken up elsewhere.

THE STEP REFLEX

Intergradation with withdrawing response.

The step reflex * is I think, merely a modification of

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The first description that I can find of the "step-reflex" is that given by Reamur (1710). After describing the morphological connection of the ampullae ("tiny pearl like" balls) and the "legs" (tube feet) he goes on to say "But one brings out the whole ingenious mechanism of it when one presses the finger on one of the "balls." It is seen to empty and at the same discussed in connection with the step reflex, a slight extension sometimes occurred due probably to an increased tension of the ampullar muscles. Next, in sequence in the non-locomotor tube feet was the retraction of the tube feet and a consequent moving of the piece of celluloid toward the ray. This does not involve release of the substrate by the disc as does the withdrawing on stimulation of the side of the column and is probably the response of the tube feet that is involved when the animal shrinks down on the substrate after having been disturbed.

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of the withdrawing reflex as a response to contact stimulation of the disk. The intergrading steps depend upon the presence to a greater or less degree of a locomotor tendency. This expresses itself, in the inverted or suspended starfish, as already shown by an orientation of the extended tube feet in the direction of the physiological anterior. If the locomotor impulse is not very strong, the only modification perhaps that will be observable in the withdrawing reaction, will be an exaggeration of the tendency to extend after the contact stimulation and before the withdrawal.

With the increase of the locomotor impulse comes a change in the behavior of the tube foot which intergrades both with the withdrawing response and the step reflex. This change is a further increase in the above noted tendency to extend, caused no doubt by an increase in the tension of the ampullar muscles. This complicates the withdrawing action, and then results, for reasons which we will take up later a more rapid contraction of the muscles on one side of the pedicel than on the other. This gives rise to a lateral movement of the tube foot which increases in extent with the increase of the locomotor impulse, from a slight bending (fig. 3) of the tube foot to one side, to an active lashing back (fig. 4) of the disk with sufficient force to throw a grain of sand some few centimeters.

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Description of the step reflex.

Under ordinary circumstances of locomotion, this lateral movement is followed by retraction and the retraction by re-extension in the direction of locomotion. This involves contact with the substrate and the stimulations which give rise to the repetition of the lashing back, the retraction and the re-extension. These movements which involve, as shown in detail later, attachment to the substrate, are those of ordinary locomotion. Each tube foot, acting independently as to time but in harmony with its fellows as to direction, repeats these movements as long as contact stimuli result from extension and the locomotor impulse remain unimpaired.

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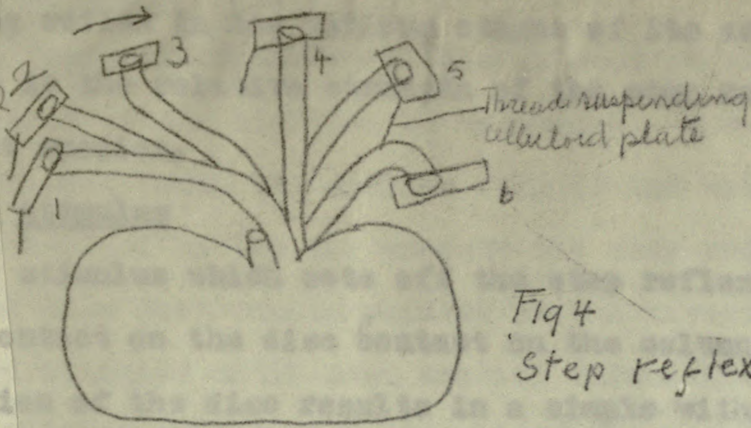
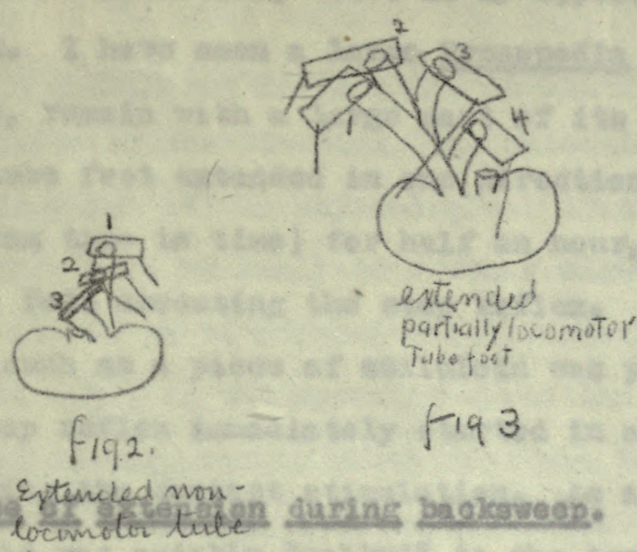
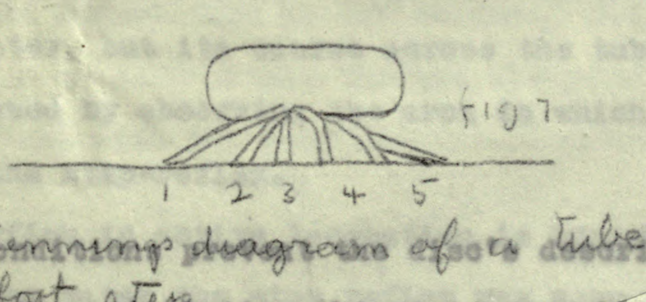



**Significance of extension during backsweep.**

Jennings (19[illegible] p. 99) describes the step reflex in terms of the behavior of a tube foot on a solid flat substrate.




Physi~~olog~~ical [illegible] describing an arc, as it does when the stimulating object is very light (See also Mangold 1908). It is this tendency to describe an arc, to keep fully extended as the disc is pushed back, that keeps the animal well off the substrate during locomotion.

A further analysis of the step reflex raises the questions

(1) What is the stimulus which sets if off? (2) what factors govern its orientation? (3) What is the status of the attaching reflex in the various stages of its accomplishment. (4) What is the relative strength of the step reflex in different species.

The stimulus

The stimulus which sets off the step reflex is one of gentle contact on the disc Contact on the column or harsh stimulation of the disc results in a simple withdrawal. In the absence of contact stimulation, there is no approach toward the step reflex. I have seen a large Pycnopodia on its back in shallow water, remain with a large part of its 22,000 (Verrill 1914) tube feet extended in one direction (the direction changing from time to time) for half an hour, with none of the tube feet executing the step reflex. When, however a light object, such as a piece of celluloid was placed on the tube feet the step reflex immediately started in all of the tube feet receiving the contact stimulation. As a result the piece of celluloid was quickly "walked" to the temporary posterior of the starfish. The same was repeated with a very thin clear glass watch-crystal. The glass could not be seen at all, under water, but its course across the tube feet could be clearly followed by observing the area in which the pedicels were executing the step-reflex.

When a starfish in active locomotion is brought above the surface of the water the step reflex was seen to occur without further stimulus. An active specimen of Pycnopodia with the ventral side exposed to the air, presents the likeness of some strange sort of military activity. With machine like regularity the 22,000 bright yellow tube feet

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The true significance of this is seen if the tube feet of a part of such a starfish be submerged. Then only those tube feet that touch the surface film of the water, or those entirely exposed to the air execute the step reflex. The submerged tube feet remain pointed in the direction of the temporary anterior until ~~some~~ contact stimulation, from the surface film or from some solid object initiates the step reflex.

<u>What factors govern the orientation of the step reflex</u>?

The first phase of the reaction, the extension of the tube foot is a function of the physiological orientation of the starfish. This will be analysed further elsewhere. Now if the lashing back is to be effective in locomotion, it must take place (as it does) in the opposite direction from the extension. This, however, merely shows that the response is adaptive and is not a physiological explanation. A physiological explanation may be looked for in the location of the contact stimulation on the disc of the tube foot or in the condition of tension in the musculature of the column. The tube foot as it extends may be seen often - though not always - to touch the substrate first with the point (fig. 6) and it may be

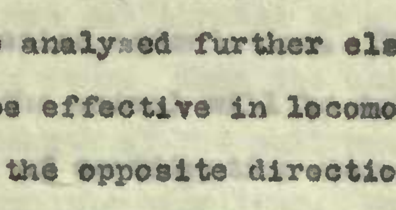


Fig 6

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expected that excitation or contraction caused by the contact stimulus might spread to the side of the column 1-3 and cause its contraction more quickly than to the side 2-4. Furthermore a contact stimulus at the place 2 does not elicit the step reflex with as much readiness and regularity (Pisaster) as a similar stimulus at the place 1. It must be remembered however that in normal locomotion the disc is often placed flat on the substrate, and that when the tube feet are exposed to the air the surface tension film may be expected to contract with equal pressure on all sides of the disc, and thus to stimulate them all equally. We have to count then upon the greater excitability of the muscles on the side 1-3 in the post-contact phase of the step reflex. This is comparable to the increased tension of the muscles on the side 2-4 in the pre-contact stage of the step reflex. The oscillations of the tube feet may be explained in terms of Von Uexküll's law of "tonus" or may be left unexplained. The fact is, of course that they move back and forth in the step-reflex with considerable regularity and precise orientation. The factors that control the orientation of the animal will be taken up in connection with an analysis of coordination among the tube feet.

<u>Status of the attaching reflex during the step reflex.</u>

The strength of attachment during the step reflex differs as we shall see with the different species and with the amount of resistance there is to the accomplishment of the step.

In general we may assume from observations on ordinary locomotion that the tendency to attach is strongest, during the progress of the step reflex, just after the contact. The tube foot usually remains attached during the first half of the backward oscillation, but the likelihood of release (or slipping) is found gradually to increase during the last phase of the step reflex.

A large grain of sand was placed on one of the ambulacral discs of an active Pycnopodia. The step reflex which resulted was so violent that the grain of sand was thrown as from a reflex with as much readiness and regularity (Piqmester) as a similar stimulus at the place 1. It must be remembered however that in normal locomotion the disc is often planed flat on the substrate, and that when the tube feet are exposed to the air the surface tension film may be expected to contrast with equal pressure on all sides of the disc, and thus to stimulate them all equally. We have to count then upon the greater excitability of the muscles on the side 1-3 in the post-contact phase of the step reflex. This is comparable to the increased tension of the muscles on the side 2-4 in the pre-contact stage of the step reflex. The oscillations of the tube feet may be explained in terms of Von Uexküll's law of "tonus" or may be left unexplained. The fact is, of course that they move back and forth in the step-reflex with considerable regularity and precise orientation. The factors that control the orientation of the animal will be taken up in connection with an analysis of coordination among the tube feet.

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A large grain of sand was placed on one of the ambulacral discs of an active *Synaptula*. The step reflex which resulted was so violent that the grain of sand was thrown as from a miniature catapult, a distance of four or five cm. On repeating this, the elevation or "angle of fire" was seen to be such as would entail release of the grain from the disc during the third quarter of the arc that the disc describes in lashing back. Usually, however, in Pisaster, Asterina etc., the violence of the lashing back is not so great, and the release is not very sudden or prompt so that such a catapulting action is not often seen in these forms.

Relation of the attaching reflex to the amount of resistance to the step.

The relation of the attaching reflex to the amount of resistance to the step was obtained in the following manner: One of the rays of an Asterina was tied by a long thread to a spring recorder which was calibrated to grams and set to write on a slowly moving drum. When the animal pulled against the spring, the strength of the pull was recorded as the height of the curve above the base line. Now when the animal had pulled the spring up to various heights, the glass plate on which it was walking was suddenly slid forward - in the direction of locomotion. This resulted in an increased tension on the starfish which was recorded on the drum until this tension became sufficient to cause the animal to release hold on the substrate. The curves got by this method were somewhat as follows:

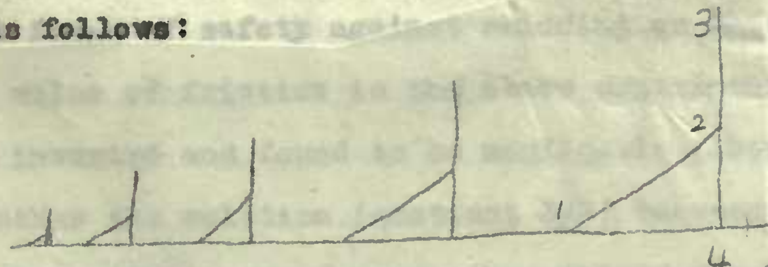


fig 5.

1-2 is the curve given by the starfish as it walks against the resistance of the spring. At 2 the glass plate was slid miniature catapult, a distance of four or five cm. On repeating this, the elevation or "angle of fire" was seen to be such as would entail release of the grain from the disc during the third quarter of the arc that the disc describes in lashing back. Usually, however, in *Pisaster*, *Asterias* etc., the violence of the lashing back is not so great, and the release is not very sudden or prompt so that such a catapulting action is not often seen in those forms.

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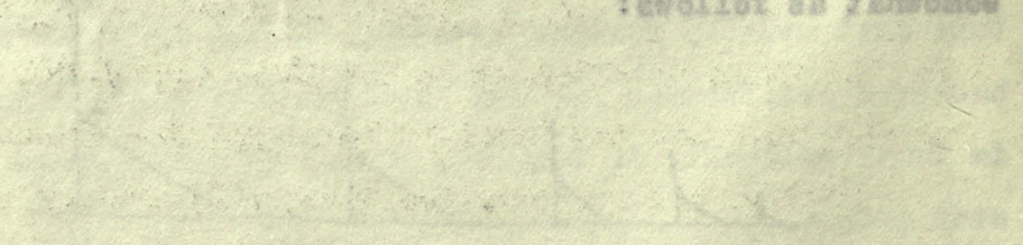

1-2 is the curve given by the starfish as it walks against the resistance of the spring. At 2 the glass plate was slid forward and the curve 2-3 measures the amount of increased pull that the starfish was able to resist before releasing (at 3).

The values for 12 observation on Asterina are as follows:

| Strength of pull (2 on fig.) | | Releases at (3 on fig.) | | 3/2 |
|---|---|---|---|---|
| 2 g | | 15 g | | 7.5 |
| 3 | | 15 | | 5 |
| 5 | | 27 | | 5.5 |
| 6 | | 21 | | 3.5 |
| 9 | | 24 | | 2.6 |
| 12 | | 36 | | 3 |
| 18 | | 45 | | |
| 18 | 18 av | 57 | 54 av | 3 |
| 18 | | 60 | | |
| 27 | | 66 | | 2.5 |
| 33 | | 84 | | 2.5 |

Disregarding the high values of the first three observations due observably to the fact that certain of the tube feet were "refractory",-that is, had not become coordinated in the step reflex and were simply attaching, we find that the strength of attachment of a tube foot is on the average 2.7 times the amount of pulling the tube foot is doing at that time (amount of resistance to the step). That is to say, the tube feet are attached strongly enough to resist a pull abut 2.7 times as great as that to which they actually are subjecting themselves; a factor of safety against skidding on the smoothest surface of 2.7. The value of friction in the above experiment was tested with the starfish inverted and found to be negligable (about 3 g).

Whether the relation (quotient 3/2) between the two variables is constant, logarithmic or of some other nature can be told only after much statistical compilation of data. In Asterina it seems to forward and the curve 2-3 measures the amount of increased pull that the starfish was able to resist before releasing (at 3).

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|---|---|---|---|---|
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| 3 | | 15 | | 5 |
| 5 | | 25 | | 5.0 |
| 6 | | 21 | | 3.5 |
| 9 | | 24 | | 2.6 |
| 12 | | 36 | | 3 |
| 13 | | 48 | | |
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Whether the relation (quotient 3/2) between the two variables is constant, logarithmic or of some other nature can be told only after much statistical compilation of data. In *Asterias* it seems to be fairly constant within the limits studied.

In Pycnopodia the relationship is even more constant, though it has a wholly different value as seen from the following table::

| Strength of pull (2 in fig.) | Release at (3 in fig.) | 3/2 |
|---|---|---|
| 9 | 18 | 2 |
| 18 | 33 | 1.8 |
| 24 | 60 | 2.5 |
| 30 | 60 | 2 |
| 36 | 72 | 2 |

Here the average quotient is 2.06. The tube foot is 2.06 times as strong to hold as it is to pull.

The difference in the value of the figure is due to specific differences between the two starfish. It is not in any way correlated with ability of the tube feet to attach when not in the locomotor state. An attached stationary Asterina is very easily removed from the substrate and only once have I seen a tube foot torn off in the process. On the other hand Pycnopodia the attachment of whose tube feet during the step reflex is much less than that of Asterina, would when in the stationary clinging state hold with such tenacity to the substrate, that it was only with much patience and the loss of many of the animals tube feet that I could pull it loose. When the starfish was once released from the substrate, if the tendency to attach continued, as it often did, I was confronted with the equally difficult and much more unpleasant task of releasing the animal from my own hands. I have spent the best part of an hour disentangling the twenty-two arms of an eighteen inch Pyconopodia from myself and the side of the aquarium.

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Strength of the step reflex (Pulling ability)

Not only does the ratio of strength of attachment to strength of pull # vary between different species, but also the pulling ability considered alone. For instance, a small specimen of Pisaster about 12 cm in diameter was attached one noon to the recording spring and induced to pull against it. During the whole afternoon the tension varied between 40 g and 60 g. The drum was removed and the animal left tugging at the thread all night. The next morning it was pulling in the same direction but had advanced slightly. The tension during that whole day varied from 95 to 190 g. There was much activity of the tube feet when the animal was going forward or being pulled back by the spring. When the animal was holding stationary tube feet were seen to be arrested in the various phases of the step reflex so that only a portion of them were extended forward at such an angle that they could pull the animal forward. Toward evening the pulling increased and somewhere between seven and nine p.m. reached a peak of

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\# Scheinmetz (1896) states that a starfish (Asterias glacialis) is able to exert a pull of 1350 g in opening a bivalve, to which pull the bivalve gave way, under experimental conditions in short order. His method of measuring the pull, however, was directed rather to measure the strength of the attaching reflex because he recorded the pull that caused a starfish to let loose its prey and not the pull which would overcome a maximal contraction of the longitudinal musculature of the tube feet. The amount of pull exerted by a tube foot, under conditions of locomotion at least, is as we have seen from one-half to one-third of the strength of attachment at that moment. Scheinmetz in this interesting paper also lists five ways in which the starfish has been supposed to open Oysters::(1) by taking the mollusc by surprise, (2) by besetting the oyster so long that it would be compelled by hunger and want of air to open,(3) by hypnotizing the molluscs, (4) by boring through their shell, (5) by poisoning them, all of which he shows are fallacious. Reamur (1710) quotes Aristotle and Pliny as attributing to the starfish a body heat, by which it kills its prey, derived no doubt by poetic analogy from the stars of heaven. He himself believed that the starfish pries open the oyster with its oral spines and sucks out the meat with its mouth.

225 g. This came from a sudden increase of pulling as shown by the curve and resulted in the arm breaking off where it was tied. The animal had thus pulled steadily at a tension of from 60 to 225 g for a period of over 33 hours. Another specimen 18 cm in diameter pulled 300 g when it was released for fear of breaking the apparatus.

Correlated with the fact that Asterina never attaches as tightly as does Pisaster is the fact that it never pulls as hard. A 10 cm Asterina, registered pulls of 60, 77, 69, and 46 g. in four successive trials. A smaller (8cm) but more active Asterina pulled 99g. The peak of the curve would be reached after a gradual ascent of about 20 minutes. The decline would last from one to two hours. Both the decline in the height of the curve and the fact that the pull did not last long, comparatively, are perhaps, evidences of fatigue.

To test the role of the attaching reflex in this response, the animal was put on sand and set to pulling in the same way. The best pull it could record was 7½ g. A 40 g.(weight in water) syracuse dish was laid on top of the animal. This increased its pulling ability to 15 g. The adding of weight to Asterina or Pisaster when pulling on a solid substrate made no appreciable difference in their pulling ability.

The case of Pycnopodia # is different as we shall see later.

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# Scheinmetz(1896) states that with respect to food taking, starfish may be divided into two types, those that swallow their food whole such as Astropecten and those that pull open the bivalves on which they feed and digest them by extruding their stomach and applying it to the soft parts of the mollusc. (Asterias) Although Pycnopodia is grouped in the Forcipulata with Asterias and has tube feet, incontradistinction to those of Astropecten, capable of tight attachment, it swallows its food whole, ejecting the undigested parts. Correlated perhaps with the fact that the animal does not pull open its bivavle prey, as do most of the other Forcipulata, is the fact that under other conditions as well, the tube feet, though they can tightly attach, do not ordinarily do so when pulling, and consequently the animal can not pull very hard.

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~~is different as we shall see later.~~ The animal studied in this respect was about 50 cm in diameter, with, according to Verrill's estimate about 22,000 tube feet, each of which was extremely active. In water the animal weighed only 50 g. but in air the weight was estimated to be well over 1000 g. Such a starfish when set to pulling against the recording lever pulled 54, 45, 30, 60 g. in four trials ( on different days). The time relations were similar to those of Asterina's pulling reaction (less than half an hour of increasing tension and up to two hours of declining tension).

The remarkable fact that this large and active starfish should not pull nearly as hard as an 8 cm Asterina, or less than one fourth as hard as a 12 cm Pisaster, was thought perhaps to be due to failure of the attaching reaction during the step-reflex, to keep the same relationship with the resistance to the step (pull) for these higher values, which it has shown according to the above table for lower levels. Some tube feet were seen to slip on the glass as they performed the step reflex. Other tube feet were seen to be in the "refractory state" that is to be attached tightly and to be showing no sign of the step reflex. This made it impossible to get direct evidence as to the status of the attaching reflex in the locomotor tube feet, as the "refractory" tube feet caused the release to be abnormally high.

Besides direct observation of slipping tube feet, indirect evidence that the lack of pull was due to failure of the attaching reflex in the active tube feet, was furnished by loading ~~"balasting"~~ the animal with 80 gm (weight under water) of syracuse dishes placed on its dorsal side. When so weighted down, the value of the 54 g. pull was increased to 69 g. and the value of the 60 gm pull was increased to 75. The increased pulling ability was undoubtedly due to increased friction between the tube feet

~~is different as we shall see later~~. The animal studied in this respect was about 50 cm in diameter, with, according to Verrill's estimate about 22,000 tube feet, each of which was extremely active. In water the animal weighed only 80 g. but in air the weight was estimated to be well over 1000 g. Such a starfish when set to pulling against the recording lever pulled 54, 45, 50, 60 g. in four trials ( on different days). The time relations were similar to those of Asterias's pulling reaction (less than half an hour of increasing tension and up to two hours of declining tension).

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On sand it was found that the animal could pull 15 gm ( without load) and with a load of 80 gm could pull about 32 gm.

COORDINATION OF THE TUBE FEET

Preliminary description.

When starfish were suspended and the tube feet at the end of one of the rays were brought in contact with some solid object, those that touched it first were usually observed to attach. Then the neighboring tube feet oriented and extended themselves in the same direction as the attached tube feet. If opportunity offered these other tube feet attached as did the first tube feet.

If now these tube feet are stimulated sharply they retract and the neighboring tube feet also retract (Romanes and Ewart 1881, Preyer 1886, etc.,). The wave of retraction passes down the stimulated arm, and out the other arms along the line of the ambulacral nervous system. This is in accordance with the older observers, especially Preyer (1886). They also showed that if the nervous system was cut at some point the above coordination would extend as far as the cut and no farther.

Further than the fact that it rests in the ambulacral nervous system, the mechanism of this coordination is very obscure. Physiologically, it is a fact attested so far as I am aware by all of the workers on this phase of echinoderm physiology. One tube foot seems to "imitate" in its activity the behavior of its neighbors. In the following analysis of coordination in the tube feet we shall inquire into its

characteristics in the rigid starfish, and compare it with the coordination manifested by the gills. We shall also inquire into coördination in tube feet of active but non-oriented starfish, the building up of this coordination into the unified impulse, the behavior of the starfish under the influence of the unified impulse and the breaking down of this unified impulse under various normal and abnormal conditions.

<u>Coordination in the tube-feet of the rigid starfish</u>

When rigid specimens of Pisaster were suspended or inverted the tube feet, after their temporary retraction from the stimulation of loosening, were found to extend more or less at right angles to the body of the ray. There were subsequent movements of the ray which will be considered later. Some of the tube feet were then stimulated to retract. There was a wave of retraction passing along the lines of the tube feet. This lessened in intensity as it proceeded from its source, so that it did not always reach the farthest tube feet. Later the tube feet would again extend the wave of extension passing back in the reverse order so that the tube feet stimulated to retract and those nearest them will be the last to reextend.

To account for this coordination in retraction and extension it is not necessary to hypothesise very complex conditions in the nervous system at the base of the pedicels. Histologically, according to Cuenot (1888), Ludwig and Haman (1899), Meyer (1916) etc., the ambulacral nervous system seems to be merely a condensation of the nerve net that extends over the outside of the myodermal sheath. So far as I am aware there is no morphological evidence of synapses in the nervous system of starfishes, though of course the evidence on this question is far from complete. A simple, nerve net will account for the above behavior.

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It has been seen that an isolated tube foot will not contract or extend quite normally. Certain conditions then may be said to exist in the nerve net at the base of the stimulated tube foot, which affect the muscles of the pedicel and ampulla and cause the normal withdrawal (or extension) of the tube foot. Now in accord with the well known laws of transmission of excitation in a nerve net (Parker 1919) these conditions may spread in any direction (within the ambulacral nervous system) and cause the retraction or extension of other tube feet. We shall see, elsewhere that no such simple condition will account for the physiological orientation of the tube feet and their coordination in locomotion.

Coordination in gills.

The physiology of movement in the gills is quite similar to that of the tube feet in the rigid starfish. Although there is lateral movement in each there is no orientation of these lateral movements in any particular direction in the gills. ~~A stimulus~~ An excitation which will cause the contraction of one group of the(dorsal) gills, will be communicated to others near these and cause ~~(Jennings 1907~~ their retraction (Jennings 1907). In this region the nerve net is quite diffuse, so that the spread of the contraction may be in any direction. The wave of re-extension usually takes a direction opposite ~~direction from~~ to that of contraction. It is centripetal rather than centrifugal. If the wave of retraction is sufficiently strong it may be communicated to the tube feet and involve their retraction as well. The retraction of the tube feet does not involve the retraction of the (ambulacral) gills (De Moor & Chapeaux 1891), an evidence of polarity in the nerve net which suggests something in the nature of a synapse. That part of the nerve net which extends up the sides of the long ambulacral gills in Pisaster also shows evidences of polarization similar to the

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Ciliary currents in gills.

One of the gills, when thus removed was seen to enclose several clumps of amoebocytes or wandering cells. These made it convenient to see the ciliary respiratory current which continued uninterruptedly after the gill had been removed. The amoebocytes moved up one side to the tip of the excised gill and down the other side to the base. It took three or four seconds to complete the circuit.

Coordination that involves some orientation of the tube feet.

Having studied the coordination of the non-locomotor tube feet and compared it with coordination of the gills we shall polarity of sea anemone tentacle (Parker 1918) in that when stimulated at the base or middle, the musculature, especially the circular musculature, below (proximal to) the locus of stimulation contracted, while that above (distal) did not contract. If stimulated at the tip the whole tentacle contracts, the circular musculature responding to a lesser stimulation than the longitudinal. If cut off at the base with scissors, the edges of both the stump and the ablated piece adhere together along the line of the cut by means, seemingly, of a sticky substance on or near the cut edges, so that the wound does not open an aperture to the exterior. The stumps of course shrivel down in strong contraction. They are found, three days later a little short but with the end healed over normally. The excised gills show no sign of contraction, and the cut end being sealed over as described above, the gill remains distended by its enclosed water like a miniature "sausage balloon" with a truncated end. The contraction of the gill musculature is not sufficient to collapse the gill against the resistance of the closed end. If this end be teased open gently and then the tip be stimulated collapse ensues immediately.

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<u>Coordination that involves some orientation of the tube feet.</u>

Having studied the coordination of the non-locomotor tube feet and compared it with coordination of the gills we shall now take up coordination in the behavior of the tube feet during their transition stages between the locomotor and the non-locomotor state.

If a rigid starfish be suspended and some of the extended tube feet be brought in contact with a solid object, as we have already seen, they will attach. This attachment is usually followed by increased activity of the neighboring tube feet and if the starfish is not too rigid, by their active bending toward the stimulated area. It is in this phase of their behavior, that the beginning of the step reflex can be elicited by proper stimulation.

Coordination to passive movements of tube feet.

If on such a starfish a long tube foot be brought in contact with a small object, such as a pencil point the disc will attach. If now, the pencil point be moved, with the tube foot still adhering so that the direction in which the tube foot is now pulled out is different from that in which it originally extended itself, other tube feet will then coordinate themselves, not in the direction of the original extension of the stimulated tube foot but rather in the direction to which it had been passively moved. This tendency to coordinate thus, while very marked in some animals, is of course apt not to show itself in starfish that are very inactive or very rigid, and is apt also not to appear at all, if there is a strongly marked coordinated impulse in some other direction. Out of thirty trials on starfish in various physiological states there was well marked and active coordination to passive movement in fifteen.

This coordination could also be brought about when the tube feet was twisted by turning the pencil a few times in the hand before pulling the tube foot over in its new direction. I could now take up coordination in the behavior of the tube feet during their transition stages between the locomotor and the non-locomotor state.

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<u>Coordination of the tube feet in the active starfish.</u>

Thus far we have been discussing coordination in the tube feet of rigid non-locomotor animals. But when a very large number of tube feet are seen in the suspended specimen, pointing in one direction in a coordinated manner, one is apt to be dealing with a starfish in the active rather than in the rigid state.

If we suspend a starfish that is active, but not definitely oriented and locomoting in any one direction, we find that the tube feet at the tips and for a centimeter or more toward the disk are oriented and actively feeling out toward the tip. Proper stimulation of the tube feet at the ends of these rays will elicit the step reflex in the direction of the tip of the ray. This would indicate that each ray has a tendency to migrate in the direction it points.

<u>Tendency of each ray to migrate toward its tip.</u>

That each ray does tend to migrate away from the disk was demonstrated by attaching five glass tubes or shell vials, large enough to accomodate the ray, to five floats and presenting these simultaneously to the tips of each of the five rays, in such a way that they could each walk onto one of the glass tubes and in so doing pull it back over the ray. When the rays got to the end of the tubes they were seen either to keep on in the same direction or reverse and back out, or part way out. It was really quite amusing to watch this suspended animal industriously observed no difference in the accuracy or promptness of the coordination. I have even manipulated the tube foot again, in its new position, without either disturbing the attachment of the tube foot or the coordination of its fellows. Needless to say these manipulations had to be done with extreme care to avoid stimulations which might cause retraction.

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Autotomy

Another indication of this tendency is the fact that in stale water or under the influance of chloroform (Moore 1916) a starfish is extremely susceptible to autotomy. Pisaster seems much more susceptible to this reaction if the nervous system has been injured in some part. As I have observed it, the reaction consists in an exaggerated tendency in the tips of the several rays to migrate in their own direction and a failure of this tendency to effect an orientation of the tube feet of the rest of the animal in the way that will be seen below to be usual in the normal starfish. This is due to a pathological sluggishness in the action of the central part of the ambulacral nervous system, as seen from the fact that the tube feet in that region are comparatively inactive. The rays of a Pisaster undergoing of autotomy present an elongated appearance. The tube feet at the tip pull actively, each in the direction of its own ray, so that after stretching somewhat the ray gives way, usually at or near the base.

FORMATION OF THE UNIFIED IMPULSE

From such a picture as the above it may seem a far call to the unified behavior of the actively walking starfish. In the latter each tube foot is put out in a single definite direction and locomotion proceeds in a beautifully unified and coordinated manner. The difference is just this, that in the unified locomotor starfish, one, or more often two adjacent rays become for some reason more active than the others and the coordinated state which is present at their tips spreads, maintaining its own direction and gaining impetus, over the other rays.

It will be our purpose now to inquire into the factors which give precedence to the activity of some ray or rays in the trying to walk in five different directions at once.

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It will be our purpose now to inquire into the factors which formation of the "unified impulse".

The responses of a starfish to stimuli, in so far as they involve locomotion, may be divided into two categories, positive responses, in which the resulting locomotion is toward the stimulus, and negative responses, in which the direction of locomotion is away from the stimulus. Gentle contact at the tip of the ray will usually elicit a positive response while a negative response usually results from severe prodding or pinching.

<u>General statement of the mechanism of the positive response.</u>

The mechanism of the positive responses, is, as I see it, as follows: A gentle contact stimulation of the tube feet at the end of a ray causes these tube feet to extend in the direction of the stimulus as we have already seen. Other tube feet behind this coordinate in this action, and receiving the contact stimulation of the substrate, execute the step reflex. The impulse to coordinate with the active tube feet at the tip of the stimulated ray thus spreads to the rest of the starfish, involving after a time every tube foot in the body in coordinated locomotion.

<u>General description of the negative response.</u>

The negative response is brought about on exactly the same principle. The prodding or pinching of a certain ray results in the retraction or inactivation of the tube feet in that region and the spread of this impulse, to certain of the other tube feet. The extent of the spread is of course determined by the strength of the stimulus.

Assuming first that the stimulation is severe enough to cause all the tube feet to retract or become inactive, ~~as we have seen~~, the first tube feet to resume their normal function are those farthest away from the source of stimulation. In this experiment the tube feet farthest away are those of the opposite ray tips. These tube feet are orineted in the direction of their formation of the "unified impulse".

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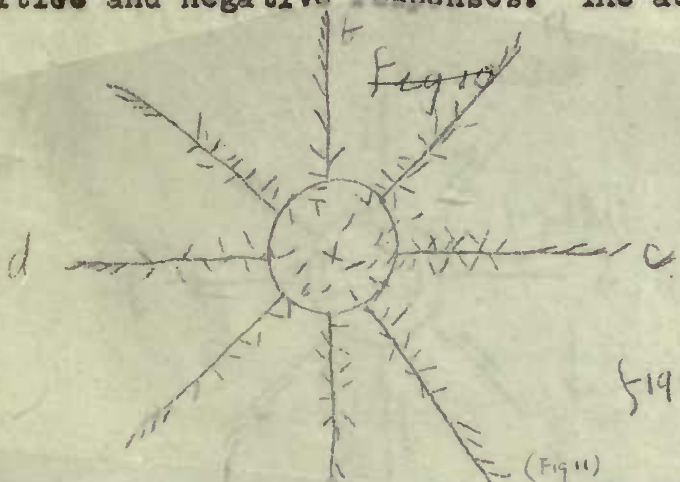
Assuming first that the stimulation is severe enough to cause all the tube feet to retract or become inactive, the first tube feet to resume their normal function are those farthest away from the source of stimulation. In this experiment the tube feet farthest away are those of the opposite ray tips. These tube feet are oriented in the direction of their which is in fact away from the source of stimulation. In so doing they come in contact with the substrate and execute the step reflex. From this point on, the coordination completes itself in the same manner as outlined for the positive response.

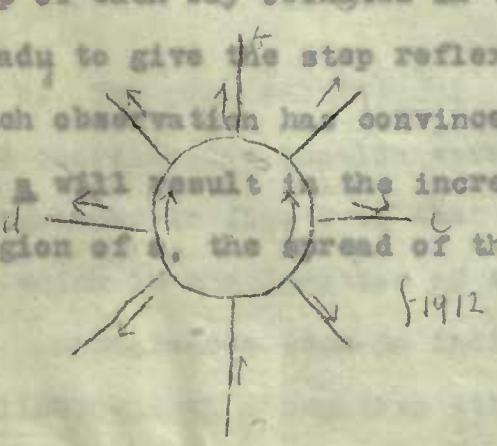
In case the stimulation is not sufficient to cause the retraction or inactivation of all the tube feet, it will spread among the tube feet, to a certain extent so that the farthest tube feet are the most active and therefore will dominate in the coordination.

Detailed description of positive and negative response in *Pycnopodia*.

*Pycnopodia* on account of its large size and great activity is very favorable for a study of the mechanism of coordination in positive and negative responses. The active but not oriented




animal can be represented as above, with the tube feet at the tip of each ray oriented in the direction of the ray, and ready to give the step reflex upon proper stimulation. Now much observation has convinced me that a positive stimulation at a will result in the increase of coordinated activity in the region of a, the spread of this coordinated activity in the way



which is in fact away from the source of stimulation. In so doing they come in contact with the substrate and execute the step reflex. From this point on, the coordination completes itself in the same manner as outlined for the positive response.

In case the stimulation is not sufficient to cause the retraction or inactivation of all the tube feet, it will spread among the tube feet, to a certain extent so that the farthest tube feet are the most active and therefore will dominate in the coordination.

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Now with the negative # response, conditions are different

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# The negative response has been described by Loeb (1900) in terms of observations by Norman (1900) as a result of the retraction of tube feet on the harshly stimulated ray and a consequent determination of the direction of the negative responses by a "parallellogram of forces" exerted by the other rays, each, hypothetically, as I take it, continuing, during the negative reaction to pull in its own direction. It is well known from the work of Romanes, Preyer, Jennings, Mangold, Cole and others that all normal locomotion is brought about by the cooperation of all of the tube feet stepping in one direction and not the divergent pulls of the various rays, which as we have seen results in autotomy.

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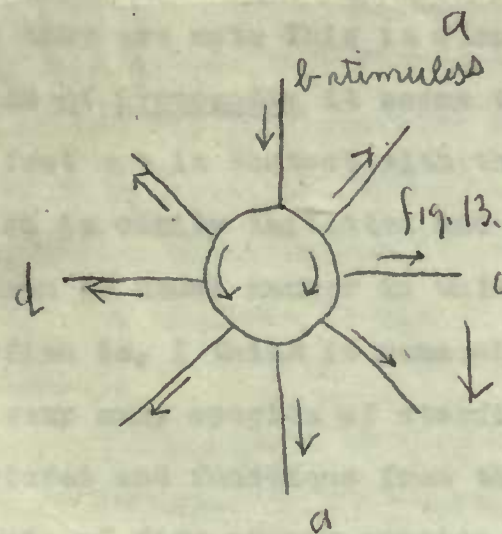


at b. The path of retraction will be as above (Fig 13) but the way the coordination impulse spreads is identical with that diagrammed in fig. 12 so that c and d become coordinated before b, which is the location of the stimulation.

Appearances seem to indicate that just after the retraction following such a negative stimulation, the tube feet on the far side of the animal show a definite increase in activity.

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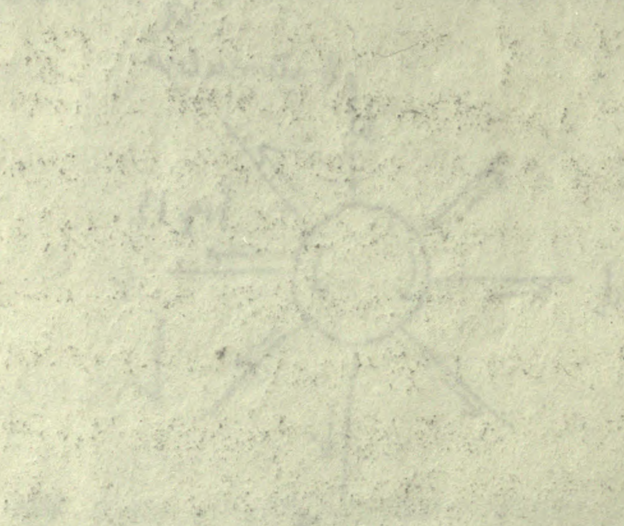

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Whether this increase is only relative or to what extënt it is absolute I am unable to say.

Function of the step reflex in the spread of coordination.

The function of the step reflex in the spread of coordination is probably very important. The pinching of one ray of an Asterina will cause prompt negative locomotion with all the tube feet coordinating. If, however, the starfish is inverted there is little likelihood that the impulse will include coordination of all the tube feet, even after the severest pinching. The only difference between the animals in these two positions is that the tube feet of the inverted starfish are not executing the step reflex because there is no contact stimulation to set it off. I am inclined to think therefore that a state of orientation spreads much more rapidly where the tube feet are executing the step reflex than where they are not. This is also true of Pisaster to a lesser extent, but in case of Pycnopodia it seems to make but little difference whether the tube feet are in contact with the substrate or not. The coordinated impulse is easily initiated and very active in this animal.

The common or usual manner in which the coordinated impulse is formed in starfish is, I think in general accord with the above outline. There are very many species of starfish, each differing more or less in its structures and functions from the other so that ideas derived from the study of five or six species might not fit the behavior of all of the thousands known to science.

I have seen Pycnopodia, Pisaster, Asterina and Evasterias regularly orient toward or away from contact and chemical stimulations (mussel juice or dilute acid) in the manner outlined above, and when a beam of direct sunlight was thrown on the eye-spot of Pycnopodia, the response was analogous to that to contact.

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In starfish which are suspended and the body wall at one side of a ray stimulated by gentle contact I have observed that the tube feet in that region show a tendency to orient themselves in the direction of the stimulus. Upon increasing the strength of the stimulation of the body wall, the tube feet near the stimulated area undergo retraction which spreads in proportion to the strngth of the stimulus. I have seen no orientation of the tube feet directly away from the stimulus even though the stimulus be graded in intensity as carefully as possible. The response is either orientation toward the stimulus or retraction.

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away from the side that is in a state of sub or super optimal illumination.

Significance of the negative behavior of the isolated ray.

The negative behavior of the isolated ray, is, as has been long known, much less definite than that of the whole animal. Romanes and Ewart ( 1881, p. 1856) state that "Single rays detached from the organism crawl sometimes away from injuries, but they do not invariably or even generally seek to escape from the latter as is so certain to be the case with the entire animals". In confirming this it was found that a migrating ray which had been isolated, would give very irregular responses to stimuli which would cause negative behavior in a normal animal. A negative response to pinching or prodding is the exception,-rather than the rule in the behavior of isolated rays. This is to be expected in the light of what has been said about the nature of the negative response because the "rays opposite the stimulus" are not there to unfailingly initiate a migration away from the stimulus.

BEHAVIOR OF THE STARFISH WHEN UNDER THE INFLUENCE OF THE UNIFIED IMPULSE

Having studied the factors which govern the formation of the "unified" impulse we shall now turn our attention to the behavior of an animal under the influence of this physiological state, first taking up the factors which cause a change in the "physiological anterior" and factors which cause a change in the direction of locomotion of the starfish by a rotation of the body as a whole without changing the anterior rays.

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The factors which cause a change in the physiological anterior are essentially the same as those which determine the anterior as the impulse is being formed and operate through the same mechanism. With respect to the sense of the reaction which they elicit they can therefore be grouped into (1) the positive and (2) the negative. With respect to the receptors on which they operate they can be grouped into (1) those acting on the dermis and directly on the tube feet and (2) those acting on the terminal tube feet of the rays (or eye spot which is a modified tube foot). Such common factors in the environment of the starfish as contact chemical stimulation and light, have been seen to effect the unified impulse in the uncoordinated starfish in one or more of the above mentioned ways and it will be seen from the following that they affect the coordinated impulse once it is started in the same sense and in the same way.

Positive reaction to contact

When one of the ray tips of a starfish migrating actively under the influence of the "unified impulse" brushed against the side of the aquarium the tube feet at the end of this ray have been seen to stretch out actively. Those behind them coordinated and soon the direction of locomotion changed and the animal was walking up the side of the aquarium

Negative reaction to contact

On pinching one of the rays of such a locomotor starfish, serial retraction or inactivation of the tube feet will ensue spreading more or less among the tube feet, but last and least effectively to the tube feet of the opposite side of the starfish. The latter resume activity first and orient more nearly in the direction of the ray on which they are borne i.e. away from the source of stimulation. The tube feet behind these coordinate themselves with them in the same direction so that the coordinated impulse (to go away from the stimulus ) spreads are essentially the same as those which determine the anterior as the impulse is being formed and operate through the same mechanism. With respect to the sense of the reaction which they elicit they can therefore be grouped into (1) the positive and (2) the negative. With respect to the receptors on which they operate they can be grouped into (1) those acting on the dermis and directly on the tube feet and (2) those acting on the terminal tube feet of the rays (or eye spot which is a modified tube foot). Such common factors in the environment of the starfish as contact, chemical stimulation and light have been seen to affect the unified impulse in the uncoordinated starfish in one or more of the above mentioned ways and it will be seen from the following that they affect the coordinated impulse once it is formed in the same sense and in the same way.

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Physiological as distinguished from physical orientation.

I have described above such changes in the direction of a locomotor starfish as involve also changes in the leading ray,- that is the animal may be going in the direction of a certain ray before the change and in the direction of the opposite rays after change. It is a matter of common observation, however, that crawling starfish sometimes change their orientation by a rotation of the body as a whole without changing the anterior ray. This is a less common method of changing direction, and is said (Bohn 1908) to be more frequent among large and stiff specimens than among small active ones.

Orientation of this kind may be called "physical orientation" to distinguish it from "physiological orientation" which involves a change of the leading ray.

Physical orientation may involve three factors, any one of which may be more or less completely predominant. These are: (1) Direct orientation of the leading ray or rays to one side: (2) acceleration of the tube feet of one side of the starfish and a consequent swinging of the anterior rays in the opposite direction: (3) the retardation of the tube feet on one side of the starfish and the consequent swinging of the anterior rays toward the same side.

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Direct orientation of the leading ray or rays to one side is dependent upon a unilateral stimulation of either the dermis, the eye spot or the tube feet of these rays and a consequent orientation of these rays toward (or away from?) the stimulus. If the stimulus acts also on the rays that are situated on the side of the starfish from which the stimulus comes, the anterior is apt to be shifted (Plessner 1913) to these arms, but if it acts only on the side of the anterior arms it is more likely to cause a rotation of the animal as a whole. This is dependent upon the angle of the stimulus to the direction of the starfish and various other factors that have been analyzed by Bohn (1908).

The relative acceleration and retardation of the lateral arms is of course a necessary result of the above described lateral movements of the anterior rays. As a result of stimulation the same factors which we have discussed above acting in a positive direction on the tube feet, dermis or eye spot would cause acceleration and in a negative direction would cause retardation, provided the stimulus did not reach the more sensitive (to a direct stimulation) tips of the anterior or posterior rays. A mechanical obstacle to the progress of the rays on one side of the animal will result in a change in orientation that may or may not involve a change in the physiological anterior. This, however, will be taken up in connection with the "deviation reaction" and the breaking up of the functional unity of the coordinated impulse.

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Theories of the mechanism of coordination.

It is probably true that all starfish locomotion involves in some of its phases at least a "unified impulse" among the tube feet in various parts of the body.

The mechanism of such coordination is of course very complex. According to Von Uexküll, in the sea urchin it involves the functioning of many nerve nets, connecting and supplying with similar "quantities" of "tonus" homologous parts of the various coordinating organs (tube feet, spines etc.,). Pending adequate histological investigations it would be well to state as an hypothesis that since homologous parts of coordinated tube feet act in almost exactly the same manner they are probably connected by nervous paths of lower threshold than are non homolgous parts. The value of such speculation, however, is dubious, and it is better to keep within the data of physiology in evaluating the coordinated impulse, since the morphological data is wanting.

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Orientation of retracted tube feet and the independence of the mechanisms of orientation and that of withdrawal or stepping.

It has been shown (Cole 1913) that the coordinated impulse may retain its orientation even after the starfish is removed from water and held inverted for two minutes. This procedure causes the retraction of the tube feet (in Pisaster) and the drooping of the arms aborally. When put back in the dish of sea water, the animal usually walks in nearly the same direction as before. This persistence of direction and the fact that the tube feet are quite retracted after each step, indicates that the mechanism of retraction and extension, of which as we have seen, the step reflex is a modification, is, perhaps, in no way dependent upon or implicated in the mechanism of orientation. The only point of contact of these two mechanisms is the fact that they both act upon the tube foot. In the locomotor state then every tube foot is oriented, whether it be retracted or not, but retracting and extending in such tube feet are accomplished usually as parts of the step reflex.

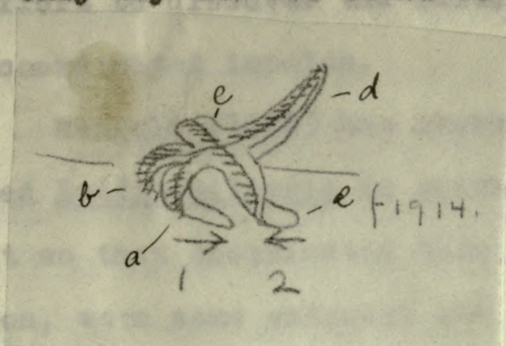
THE BREAKING UP OF THE COORDINATED IMPULSE INTO AREAS IN WHICH THE TUBE FEET ARE ORIENTED IN DIFFERENT DIRECTIONS.

Perhaps the most puzzling thing about the unified impulse is the fact that under certain conditions it may be broken up so that it may exist in only a part of the starfish, or tube feet of different parts of the animal become oriented in different directions.

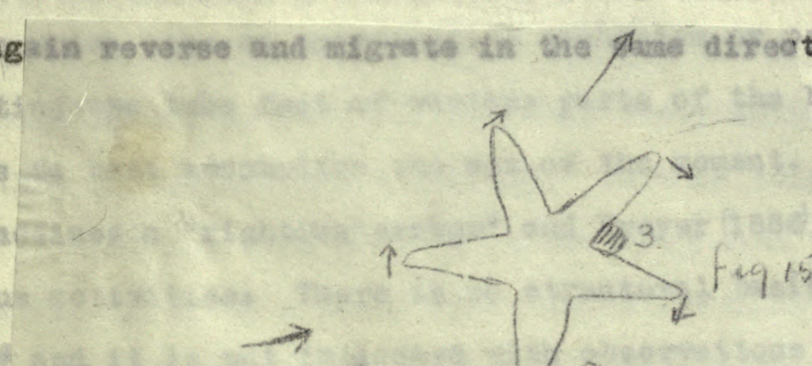
Adaptiveness

In case of some types (Jennings 1907) of the righting reaction, and in going around an obstacle this orienting of

the tube feet in different parts of the starfish in different and sometimes oppostie directions is highly adaptive in that it is the only way the act could be accomplished.




Thus in the above diagram, fig. 14 which illustrates a frequently observed type of righting reaction the rays labeled a b have doubled under and are migrating in the direction of the arrow. The rays labeled c e under the influence of the same unified impulse have turned in the same direction but migrate, after having turned, in the opposite direction, thus crossing over the arms a b and completing the somersault. As soon as the righting is complete the rays c e again reverse and migrate in the same direction as the rays a b.




When, (fig. 15) the starfish was in position 1 it was moving in the direction of the arrow and all of the tube feet were oriented in this direction. However, when coming up against the obstacle (3) the tube feet of each ray immediately changed their orientation to the direction indicated by the arrows at the tips of the respective rays. This results in the

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Mangold (1908) has described an observation in the slender armed <u>Luidia ciliaris</u> in which the animal was seen to have an arm bent so that coordinated tube feet, all extending in the same direction, were some extended out to the right of the ray, some parallel with the ray and some to the left of the ray.

fig 14a

If we are to explain this very puzzling behavior from a physiological standpoint we can not merely point out its adaptive or regulatory value, we must attempt an analysis of its mechanism. It is futile also, to conjure up a complex "center" in the nervous system which acts as coordinating mechanism or presiding regulator, orienting the tube feet of various parts of the body in such a manner as to best accomplish the act of the moment. Steiner (1898) hypothesizes a "righting center" and Preyer (1886) "centers" for various activities. There is no structural basis for such an assumption # and it is not in accord with observations on the behavior of

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nimal nearly avoiding the obstacle and migrating off in the irection indicated by the upper arrow. This is a very interesting reaction and has been made the subject of careful study below n an effort to discover the factors concerned in this breaking up f the coordinated impulse.

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the tube feet which seem to indicate that they all act very much like their neighbors, but with too much independence to lead to the belief that they are subject to the control of a higher center. Tube feet act only in response to stimuli which affect them or spread to them from neighboring tube feet.

Possible physiological explanation in the traction on the tube feet resulting from the movement of the rays over the substrate.

It seems to me that the only constant factor that could account for the behavior observed, is the traction of the substrate on the tube feet. This traction is the mechanical result of the movement of the starfish over the substrate. (See Cole 1913b).

Thus Mangold's starfish (fig. 14a) is moving in the direction of the arrow. The various tube feet may receive stimuli from the substrate which result in their orienting in this direction.

Similarly the righting starfish has set in action by the activity of the rays a and b (fig. 14) a somersaulting motion on a horizontal axis. This results in pulling the rays, c and e in the direction of the arrow that indicates their motion. It is this traction that may orient the tube feet. In this connection it is to be noted that if the rays c and e do not droop down to the substrate but are carried over at a level of or above the disk ( as is more often the case) their coordinated impulse does not reverse but remains, as indicated by the parallel extension of the tube feet, in harmony with that of the rest of the animal.

In the case of the deviating starfish, the axis of the rotation that is involved in the avoiding of the obstacle is of course the obstacle itself. There is, in the progress of the reaction first a pushing against the obstacle which involves cessation of locomotion on the part of the rays on one side of the body, but its continuation ( or quick resumption after temporary cessation) the tube feet which seem to indicate that they all act very much like their neighbors, but with too much independence to lead to the belief that they are subject to the control of a higher center. Tube feet act only in response to stimuli which affect them or spread to them from neighboring tube feet.

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Direct pull, exerted through the substrate by the movement of the animal and acting on the tube feet, can, assuming that it orients them, account for the above described behavior. We shall now turn to the evidence for and against the contention that the pull of the substrate does orient the tube feet.

Direct evidence inconslusive.

The obvious way of testing this is to slowly pull the animals over the stubstrate (see Cole 1913b) and ascertain whether a tendency to locomotion in this direction could be built up. About forty trials were made with rigid non-locomotor animals. The tube feet at first caught hold and clung to the substrate. This became less and less manifest and the rigidity of the myodermal sheath gave place to the flexibility that usually accompanies locomotion. Locomotion followed, however, in less than half the trials, the animal more often settling down obstinately in the place to which it was pushed.

When the locomotion did follow, it was, unfortunately, in every case but one in the opposite direction to the pull. It continued for a few cm. only, when the animal would settle down into the rigid state. The one animal that crawled in the direction in which it was pulled, continued to crawl all day.

These results were complicated by the effects of contact stimulation of the dorsal surfaces which induces close attachment and cessation of locomotion. The reactions of the animals, then for the most part may be considered a result of this stimulation rather than a result of the pull.

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These results were complicated by the effects of contact stimulation of the dorsal surfaces which induces close attachment and cessation of locomotion. The reactions of the animals, then for the most part may be considered a result of this stimulation rather than a result of the pull.

I have in fact been unable to manipulate the starfish so as to exert a steady pull in any one direction for any length of time without causing the tube feet to attach and hold on, a tendency which then spread to other tube feet and inhibited any coordinated impulse that might have resulted. Later, moreover, on certain occasions they have been observed to retract and be entirely inactive.

I have manipulated the animals by slowly moving the substrates on which one or two rays were walking and have manipulated them by means of neurotomized or anaesthetized rays but have not been able to do so with enough delicacy to avoid stimulating the tube feet to become attached or completely retracted. I am inclined, therefore, to consider these results irrelevant rather than evidence against the possibility that the substrate may have an orienting influence upon the tube feet.

Evidence from neurotomized animals.

If the substrate can orient the tube feet by exerting a directive pull on them through the movements of the animal, we might expect to find that if one of the posterior arms of a loconotor starfish were neurotomized, there might be coordination brough about by the factor in question. Several experiments were performed with it in view to test this hypothesis, the results of which were complicated by the marked tendency in the injured animals to attach closely and firmly to the substrate.

The operation was performed on a large, active Pycnopodia. At first the tube feet on the injured arm attached but the movement of the animal wrenched the tube feet loose leaving in one or two cases the disk affixed to the substrate. As the locomotion continued the tube feet stuck less and less

tightly, until they behaved very much like they do in ordinary but rather inactive locomotion. The arm being very flexible, coordination did not occur when the neurotomized arem was anterior, because it bent around and under before the tube feet let loose. Some three or four hours after the operation the tube feet in the neuromotized arm were all retracted and the arm practically motionless. A week later the wound seemed to have healed and the arm to have regained its natural movements.

When this experiment was repeated on Pisaster, the animal remained stationary for five minutes, the neurotomized ray, affixing itself rather firmly to the substrate. At the end of this time the other rays were seen pulling in the direction of their former anterior, away from the neurotomized ray. Some refractory tube feet were seen attaching to the substrate, which were wrenched off by the activety of the uninjured arms. One left its disc behind. Refractory feet became fewer and less refractory. In one minute coordination was complete, though not very active. The animal walked quite rapidly the length of the aquarium. Locomotion seemed normal except that the neurotomized arm was catracted and rigid. It was always behind or obliquely behind in locomotion.

It might seem possible therefore that coordination of the tube feet is not wholly dependent upon the presence of an intact nervous system. If such stimuli as cause the attaching reflex, are carefully excluded coordination may be established, across a cut nerve cord by the traction of the other arms.

When the neurotomized starfish had come to rest it was observed that the four intact rays were stationary while the neuro-tomoized ray walked about in the sector between the adjacent stationary rays. I Then prodded the starfish and threw it into a slightly, until they behaved very much like they do in ordinary but rather inactive locomotion. The arm being very flexible, coordination did not occur when the neurotomized arm was anterior, because it bent around and under before the tube feet let loose. Some three or four hours after the operation the tube feet in the neurotomized arm were all retracted and the arm practically motionless. A week later the wound seemed to have healed and the arm to have regained its natural movements.

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I believe, therefore, that neural connection for the spreading of an impulse across the cut, either through the dermal nerve net or through an uncut portion of the ambulacral cord, was entirely absent.

The essentials of these esperiments were repeated on a number of animals, with very similar results. Asterina responds in this way but rather less completely than Pisaster.

An active starfish with a e anterior (see fig 16 p 55) was picked up quicly and the rays b c d neurotomized. The animal was set on the side of the aquarium with the intact rays (a e) directed downwards. Locomotion followed a e down the side and across the aquarium. B c d presented refractory tube feet and locomotion was jerky as these tube feet were pulled loose. Later, when the animal had progressed about 6 cm coordination was fairly well established but not very active. As the refractory tube feet were pulled loose they retracted and did not react at all, for sometime. Neighboring tube feet, however, showed diminished tendency to attach tightly and were more apt to coordinate. Locomotion was slow at first but later more rapid.

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An active starfish with *a e* anterior (see p. 155) was picked up quickly and the rays *b c d* neurotomized. The animal was set on the side of the aquarium with the intact rays (*a e*) directed downwards. Locomotion followed *a e* down the side and across the aquarium. *B c d* presented refractory tube feet and locomotion was jerky as these tube feet were pulled loose. Later, when the animal had progressed about 6 cm coordination was fairly well established but not very active. As the refractory tube feet were pulled loose they retracted and did not react at all, for sometime. Neighboring tube feet, however, showed diminished tendency to attach tightly and were more apt to coordinate. Locomotion was slow at first but later more rapid.

I next neurotomized (near the base) each arm of a rather large starfish that was not very active. I "started" it on the side of the aquarium with its former "anterior" downward. Locomotion continued down the side until the disc was about at the angle of the wall with the floor of the aquarium. At this point, the animal assumed the rigid state and would crawl no farther.

This experiment was repeated on a smaller and more active specimen. Locomotion down the side was more active, the ~~leveling~~ leading (former anterior) arm taking up the locomotion quickly and by pulling, in harmony with the force of gravity, forced a certain amount of coordination in the other rays. There were a few refractory tube feet in each of the rays, each ray showing a tendency to migrate toward its own tip. When the animal reached the angle of the side with the floor of the aquarium the locomotor impulse was so well established that crawling continued across the floor of the aquarium and up the other side. If an obstacle such as my finger was placed between the two anterior rays and held stationary, two responses were observed. In two cases a normal deviation reaction ensued, but the more frequent result was a stoppage of locomotion followed after a variable length of time by a resumption of locomotion in some other direction.

The starfish was then taken up and stimulated harshly on the various rays. The animal assumed the rigid state when set down the tube feet being tightly attached, and remained in this state for some time. The rays, a and c, that became active first were not contiguous, ~~a and c~~, while b d and e remained attached. A and c moved about in their sectors at random all the afternoon. The next morning the starfish was in a moribund condition but had migrated across the aquarium during the night.

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The essentials of these experiments were repeated many times with results that varied between the two examples cited. It was found that if the manipulation was rough or unnecessarily prolonged, the animals would become rigidly attached and would not locomote for some time or at all while some animals refused to coordinate with even the gentlest manipulation.#

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# Opinion on the necessity of an intact nervous system for echinoderm coordination seems divided. Romanes and Ewart (1881) and Cole (1913) record some slow coordination between parts on opposite sides of a cut in the nervous system, while Russo (1913) believes that coordination may be absolutely normal with the oral nerve ring removed. Clark (1899) states that the coordinated movements of the tentacles in *Synapta* and coordinated movements of the body muscles are not destroyed by cutting the nerve ring. See also Grave 1900 on *Ophuira brevispina*

Among those who report the opposite results are Vulpian (1862) Krukeuberg (1881) DeMoor and Chapeaux 1891 Loeb (1900). Mangold (1908a 1909a) Moore (1910a, 1910b) etc

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From these experiments, and those on the righting of neurotomized animals which will be described later, I think that it can be safely concluded that while there is no neural or "neuroid" (Parker 1919) transmission past a cut in the ambulacral nervous system, there may be a certain limited amount of coordination between parts separated by such a cut brought about through their mutual relationships to the substrate.

*Evidence from the behavior of the animal when its parts are placed on separate substrates.*

We shall turn now to such indirect evidence as bears upon this point from the behavior of an animal on separate substrates and to a quantitative analysis of the mechanics of the deviation reaction. These methods, though indirect do not cause the attaching reaction.

The rays of an active starfish that is not in the coordinated state, as has been seen above will migrate toward their tips, into free floating glass tubes. If however before suspending and before the floats are presented to the rays, the animal was in a state times with results that varied between the two examples cited. It was found that if the manipulation was rough or unnecessarily prolonged, the animals would become rigidly attached and would not locomote for some time or at all while some animals refused to coordinate with even the gentlest manipulation.§

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Supplementary experiments were carried on with flat free swinging substrates. One, two or three of the rays were put on the substrate and the others allowed to hang over the side on the floor of the aquarium half a cm. below. The part on one substrate was often seen to migrate while that on the other remained stationary, and they were not infrequently seen to migrate in different directions. Of course this would not be likely to happen if the substrates were not separately moveable.

From the above experiments it would seem that a factor in the unity of the coordinated impulse is the unity of the substrate or rather of the animals relation to the substrate.

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# One might state the case rather paradoxically in metaphysical terms by saying that the animal's soul or entelechy, or some part of it at least resides in its substrate. (See Dreisch (1908) Sterne (1891).)

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Therefore, if the activity of the animal caused the substrate to move in one direction with reference to one part and in another direction with reference to another part, as is the case in the righting and deviation reaction, we might expect that the unified impulse would be broken up in certain determinate ways.

<u>Deviation reaction not interfered with by cutting nervous connections with interradial area.</u>

That the coordinated impulse is thus broken up by mechanical traction in the deviation reaction, is made likely by the fact that the reaction is perfectly normal even after the nerve net on the outside of the epidermis was cut through between the obstacle and the ambulacral nervous system. This, of course prevented any stimulus from the contact of the starfish with the obstacle reaching the tube feet, but did not affect the mechanical factors in the relation of the substrate with the tube feet. It is therefore to be concluded that these mechanical factors play an important role in the deviation reaction.

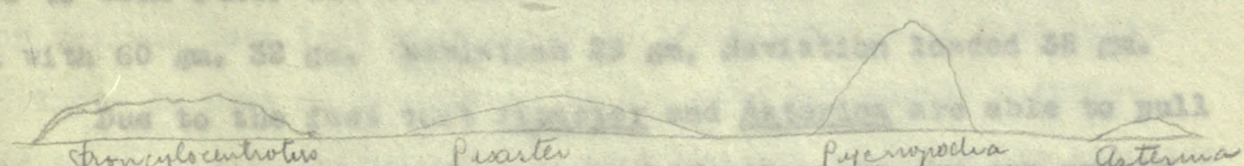
<u>Deviation reaction not elicited by prodding interradial area.</u>

Moreover, if the nerve net between the bases of the two anterior rays be stimulated by jabbing it quickly with a knife or a blunt instrument, the deviation reaction will not follow. The animal will either continue undisturbed, stop and then continue or go into the attached condition and remain so more or less permanently. The first response is by far the most common if the specimen is normally active and not stimulated too harshly. I have never observed a marked change of direction as is seen in the deviation reaction to say nothing of the

complicated coordination of movements that are involved in the deviation reaction.

<u>Quantitative aspects of the "deviation push" on different substrates and with different weights on the animal vary with mechanical conditions while quantitative aspects of contact stimuli required to initiate the negative reaction do not.</u>

It was thought that the amount of push which the deviating animal exerted upon the obstacle when considered in connection with its pulling ability, and other reactions might throw light upon the mechanisms of the deviation reaction. The amount of push was measured by attaching the obstacle, a lever, swinging freely from a rigid fulcrum by a thread to the recording spring above described. The push, then was recorded as the height of the curve, written on the slowly revolving drum. The appearance of the curve was as below for the different species studied.




The push continues to increase until the deviation begins, that is, until the effectors (tube feet or spines) on one side of the body begin to reverse themselves and the rotation around the obstacle as an axis is initiated. From then on there is an irregular decline in the push until the animal is free of the obstacle. With the drum running at the same speed, the shape of the curve as well as its height is dependent upon the activity of the specimen studied. This was taken into account so as to get results as comparable as possible. ¶The sea urchin <u>Strongylocentrotus</u> <u>franciscanus</u> was found to be moving on sand by means of its spines only. In deviating around an obstacle complicated coordination of movements that are involved in the deviation reaction.

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The value of the "deviation push" of this specimen, was found to average 13 g. This was increased to 17 g when a load (about 40 g) was placed on the dorsal side of the animal. The "pulling ability" was found to be (average of 6 trials) 10 g unloaded and 15 g loaded. Allowing for a certain amount of fatigue in the later trials the "pulling ability" was found to be approximately equal to the "deviation push".

The same relationship seems to hold with Pycnopodia. As seen above the pulling ability averages 47 g. the deviation reaction (average of four trials 60 g 45 g 60 g 30 g) is 48g. These are increased to 72 and 105 g respectively by loading the animal with 80 g. of glassware. If the animal is placed on sand the values are similarly related to each other but are reduced as follows. Pulling 15 gm, pull-loaded with 80 gm. 32 gm, deviation 29 gm, deviation loaded 35 gm.

Due to the fact that Pisaster and Asterina are able to pull very much harder in proportion to their size than are the sea urchin or Pycnopodia and since this pull is due to the constant increase of the attaching tendency correlated with the pull, we find that the deviation push correlates more closely with the pulling ability on sand, taking into account of course its lesser frictional coefficient, than with the pulling reaction on a solid substrate. The average deviation push of Pisaster (about 15 cm in diameter) is 20 g. on a solid substrate and 6 g on sand. Asterina (8 cm) on a solid substrate exerts a deviation push of 4 g, but with 4 g. weight on its back this is increased to 6 g. This is comparable with the pulling ability of a larger specimen on sand of 7.5g.

and on sand weighted (40g) of 15 g (See p. 21). The above study of the mechanics of the deviation does not pretent to be statistically comprehensive. The object is merely to point out that the "deviation push" can be always increased by weighting down the animal and that in the sea urchin, which uses its spines, and in Pycnopodia which does not attach tightly while pulling hard (See p. 22) the pull can also be increased by weighting down the animal. The relationships of pull, and deviation push in the loaded and unloaded Asterina and Pisaster, are consistent with the above and comparable, quantitatively to the pulling ability of the animals, both loaded and unloaded on sand.

Thus, the attaching reflex that strengthens with the resistance to the ordinary step (see p. 19) does not appear comparably in the deviation reaction. This it seems to me is because the tube feet on one side of the obstacle overbalance in their traction those on the other side, cause a rotation of the animal in that direction and the various tube feet coordinate in the direction of this rotation. There is then no resistance to the step but merely a deviation of it in one direction or the other brought about by its relation to the substrate.

Another fact pointing to the conclusion that the factors of the deviation reaction have to do with the mechanical relationship of animal to substrate rather than with reflexes having their receptors at the point of contact is that if the tips (Asterina) of the rays instead of the dermis between the rays come in contact with one obstacle connected with the spring recorder the amount of pressure that it takes to cause a change in direction, does not vary if a weight is put on the back of the starfish. The value is about 2.5 g in each case. This shows nd on sand weighted (40g) of 15 g (See p. 21). The above study f the mechanics of the deviation does not pretent to be statisti- ally comprehensive. The object is merely to point out that the deviation push" can be always increased by weighting down the animal nd that in the sea urchin, which uses its spines, and in Pycnopodia hich does not attach tightly while pulling hard (See p. 22) the pull an also be increased by weighting down the animal. The relation- hips of pull, and deviation push in the loaded and unloaded Asterina nd Pisaster, are consistent with the above and comparable, quanti- atively to the pulling ability of the animals, both loaded and un- oaded on sand.

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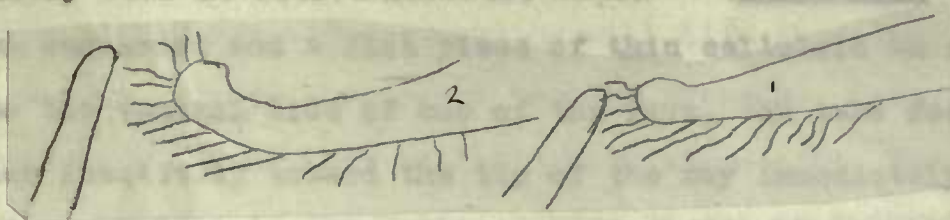
In order that the obstacle may be left behind in the deviation reaction there is usually a turn of at least $70^{\circ}$ which is often recovered from, by the operation of a tendency, whose mechanism I have not worked out, to continue crawling in the same direction as before the disturbance, even if the action involve an actual change of direction, back, from one assumed as the result of the disturbance. This tendency will also be noticed in connection with the righting reaction (p.75).

## COORDINATION OF MOVEMENTS OF THE TUBE FEET WITH THOSE OF THE ARM AS A WHOLE

Illustrations of the tendency of an arm to set itself more at right angles to its actively oriented tube feet, when such movements involve dorsal and ventral flexion and lateral twisting.

If an active starfish be suspended and a solid object be brought in contact with the tip of one of the rays, there will be a movement of the tube feet in the direction

of the object, an activation of their coordination toward the tip of the ray. This will be followed, almost immediately by a dorso-flexion of the tip of the ray. The ray can be said to set itself more nearly at right angles to the ~~extended~~ oriented active tube feet. This reaction has been observed time and again in <u>Pisaster oraceum</u>, <u>Asterina</u>, <u>Pycnopodia</u>, <u>Leptasterias</u>, <u>Pister bre-vigpinus</u> and <u>Evasteriaz</u>. As are most movements of the animal it is a product of local reflexes in that it is not dependent upon connection with the oral nerve ring, but occurs equally well in active isolated arms.




¶ If, for the gentle contact we substitute a harsh tapping of the tip of the ray, the tube feet will retract and the ray become more rigid and shorter, but without any sign of the dorsal flexion.

¶ We have seen that if a tube foot in the middle of a ray be allowed to attach to an object and the object be then pulled to one side, the tube foot with it, other tube feet will also move to the same side and seemingly reach out for the object to which the tube foot is attached. Now if a sufficient number of tube feet become oriented in this manner, there will be a lateral twist of the ray toward the object. Here again the of the object, an activation of their coordination toward the tip of the ray. This will be followed, almost immediately by a dorso-flexion of the tip of the ray. The ray can be said to set itself more nearly at right angles to the ~~extended~~ oriented active tube feet. This reaction has been observed time and again in *Pisaster ochraceus*, *Asterias*, *Pycnopodia*, *Leptasterias*, *Pisaster brevispinus* and *Evasterias*. As are most movements of the animal it is a product of local reflexes in that it is not dependent upon connection with the oral nerve ring, but occurs equally well in isolated arms.

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fig 17

(See also Jennings (1907) description of the taking of food from the pedicellariae by the tube feet).

When The slender armed species of starfish (<u>Evastinias troschelii</u>) was suspended and a flat piece of thin celluloid was swung by a thread to the ventral side of one of the rays, the tube feet, oriented rather inactively toward the tip of the ray immediately sieze the object and "walk" it in the direction of the base. This was observed to involve the orientation toward the object of quite a number of tube feet both above and below it and the bending of the ray so as to receive the object in a sort of hollow. The tube feet in actual contact with the object are,

of course, undergoing the step-reflex, but above and below, where the tube feet are all directed toward the object, it can be said, again that the ray tends to set itself more at right angles to actively oriented tube feet, this time involving both dorsal and ventral flexion. In the region where the tube feet are undergoing the step-reflex, there is no bending of the ray.#

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# It has been shown by both Jennings (1907) and Mangold (1908a)

that as the tube feet carry a small piece of food toward the mouth there is a "humping up" of the ray in the region of the food which probably involves the factors described above. The behavior of the tube feet when the animal moves its arm in under the disc as a part of the food taking response (Jennings 1907) would be interesting but I have never been able to induce this response in the species at hand.

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Ventral flexion of rigid, of injured and nicotinized starfish

If a Pisaster in a state of extreme rigidity be inverted there will be as we have seen, a rather inactive extension of the tube feet more or less at right angles to the rays. There will be no orientation of the tube feet at the tip in the direction of the ray. The rays, soon after inverting will lift themselves orally and assume a very symetrical ventral flexion. This state may continue, in absence of disturbing stimulation for as much as twelve hours. If the radial nerves be cut or injured near the base, this ventro flexion is apt to be very much intensified so that the steps of the rays come nearly or quite in contact and the animal assumes what Romanes ~~(1881)~~ and Ewart (1881) who describe this response aptly call " a tulip like form". This is similar to the state of ventro flexion which Moore (1920a) # describes as a result of nicotine poisoning, and

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which I have confirmed for Pisaster. The chief difference seems to be that the tube feet in the nicotinized Pisaster are completely retracted, while those of the rigid, or of the neurotomized animal show a certain amount of extension but no particular orientation. The strength of the spasm is greater in the nicotinized animal.

These movements are shown by the isolated ray from both the nicotinized (Moore) and the rigid animal.

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Description of various other correlated movements of the tube feet and arms.

If an active Pisaster be suspended in water and away from contact stimulation, the rays move about for a while, flexing themselves dorsally and laterally, in a manner that we shall discuss later, but eventually assume a state of ventro-flexion similar to that assumed by the rigid animal. The active animal in ventro flexion differs, however, from the rigid or the nicotinized animal in that contact stimulations at once set up activities of the tube feet and arms. The tube feet react positively to gentle contact stimulation and retract upon severe stimulation. We have followed the immediate responses of the arms to these stimulations, but the positive and negative activities of the tube feet spread to the tube feet of the rest of the animal, as also do the corresponding movements of the arms. Thus if the stimulation be quite harsh the tube feet will retract over the whole animal and the arms themselves will become shorter and more rigid.

In connection with the positive response of the tube feet, ir will be remembered that this does not spread as well when the tube feet are free from contact as it does when they are executing the step reflex. A weak positive response then, such as the positive differential activity of the unstimulated arms in case of a harshly stimulated animal, hardly makes itself noticeable in the suspended animal as it does in the negative response of the animal locomoting on a substrate.

Description of the formation of the coordinated impulse when the tube feet are free of the substrate.

A strong positive response, on the other hand, does spread, and in spreading involves movements of the arm, as the following experiment will show. An active Pisaster suspended and in a state of

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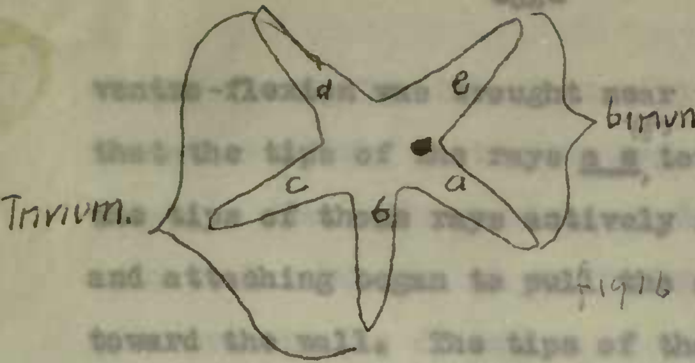


ventro-flexion was brought near the side of the aquarium so that the tips of the rays a e touched the wall. The tube feet at the tips of these rays actively stretched out toward the wall, and attaching began to pull the starfish still farther over toward the wall. The tips of the rays a e flexed dorsally and began migrating in their own direction. In the meantime the coordination of the tube feet had spread so as to include all the extended tube feet in the animal, which were soon all pointed directly toward the wall of the aquarium. As the tube feet became oriented in this direction, there was a coordinated movement of the rays. Ray b twisted to the left and bent over toward the wall, ray d twisted to the right and bent over to the wall and ray c bent directly over the disc toward the wall. Each ray was seen to set itself more at right angles to the actively ~~extended~~ oriented tube feet which had become coordinatedly pointing toward the wall.

As the rays a e continued their activity, the disc was brought closer to the wall and with it, the other arms. As they touched the wall, since the tube feet were oriented in the direction of a e they began executing the step reflex in this direction and the animal started perfectly coordinated and normal locomotion in the direction of a e (the suspending thread having been cut)

Correlation of these movements with the righting reaction.

The above experiment is merely a simplification of the righting reaction of the uncoordinated active *Pisaster*. If we assume that two adjacent rays initiate the reaction by attaching to the substrate with their ventral sides turned toward each other, the above description will fit the righting reaction with the change of only a few words. The same dorsal flexion of the initating rays and their migration toward their tips will ventro-flexion was brought near the side of the aquarium so that the tips of the rays a e (tips) touch the wall. The tube feet at the tips of those rays actively stretched out toward the wall, and attaching began to pull the starfish still farther over toward the wall. The tips of the rays a e flexed dorsally and began migrating in their own direction. In the meantime the coordination of the tube feet had spread so as to include all the extended tube feet in animal, which were soon all pointed directly toward the wall of the aquarium. As the tube feet became oriented in this direction, there was a coordinated movement of the rays. Ray b twisted to the left and bent over toward the wall, ray d twisted to the right and bent over to the wall and ray c bent directly over the disc toward the wall. Each ray was seen to set itself more at right angles to the actively ~~extended~~ oriented tube feet which had become coordinatedly pointing toward the wall.

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be observed. The tube feet will all coordinate pointing in the direction of the initiating rays and the other rays will move so as to come more at right angles to the direction of the tube feet. The arm on the right will twist to the right, and move over in the direction of the initiating rays. The arm on the left will twist to the left and do the same thing. The arm directly opposite the initiating arms will bend directly over the disk and complete the somersault with locomotion, as we shall show later, continuing generally in the direction of the initiating rays. This as we shall see is perhaps the most common method of righting at the disposal of the starfish.

Analysis of Jenning's Seven types of Righting reaction.

Jennings (1907 pp. 125 ff ) however, describes seven main types about which the extremely variable righting reaction may be grouped. The first type is:

1. "The simplest and neatest method is the following. Two adjacent rays twist their tips in such a way that the ventral surfaces of the two face each other. Then the tube feet of these rays attach themselves and throw the starfish over in a neat somersault."

This is essentially the method described by me above. Jennings description leaves out, here, the coordinated action of the unattached arms though he mentions it elsewhere in general terms, and he does not recognize the spread of the coordination among the tube feet nor its relation to the movements of the arms. As above stated this is the commonest method of turning. We shall inquire as to the reason for the turning of the rays toward each other in a majority of cases in connection with our discussion of the righting of the oriented starfish.

Jennings second type is as follows.

2. "The tips of the two adjacent rays may so twist that the ventral surfaces do not face each other, but both face in the same direction. The tube feet then take hold and throw the starfish over, twisting it about an axis which passes lengthwise through one of the attached rays. This method of turning is extremely difficult and awkward but is seen at times. Usually however a third ray takes hold and aids in the turning, the method then forming a transition to that given next."

I have observed this method of righting only a few times, and variations of it (Type 5 (6) of Jennings) where only one ray attaches a few times also. In each case the coordinated impulse could be seen to spread from the initiating ray or rays and involve coordination of the rest of the tube feet and to some extend the arms in the manner described above. The ray that might be expected to attach coordinately (facing) the ray that bends down is usually seen lifted above the substrate and reaching out in the direction of the righting. Locomotion after righting is usually toward the rays that initiate the reaction.

Jenning's third type is as follows.

3."Three adjacent rays attach and remain attached, all pulling throughout the reaction. Usually the animal turns primarily by the aid of the two outer rays, while the middle one is relatively passive and compelled to double back under as the animal turns. Often this middle ray walks backward beneath one of the other rays, or the other walks actively over its surface, or there is a combination of these two movements tillthe normal position is reached. ( A model of the starfish in paper or cloth will make clear the necessity of such movements when three of the rays remain attached.)"

There is no new principal involved here, except that of

the passive (!) movement of the middle ray which will be discussed in connection with the fourths type. The impulse spreads to the tube feet of the two unattached rays. The coordination of these is followed by their raising up over the disc and moving toward the initiating rays in the same way and according to the same principles as described above. (types 1 and 2).

The fourth type is as follows.

4. "Four of the rays take hold, two extending to the right, two to the left. Then the fifth ray, (which we may call the posterior one) is lifted straight up and swings directly over till its ventral surface reaches the bottom, while the anterior attached pair walks backward beneath the posterior attached pair the latter walking forward over the surface of the (former)"

This type of righting is sketched ~~on p.~~ fig 14 In case of Pisaster it is more apt to occur if the animal is very much relaxed. The sequence of the events as I have observed it is as follows, The anterior rays twist toward each other and the coordinated impulse spreads over (or is already in) the starfish as in type 1. This results in the twisting toward them of the lateral rays and the bending up of the posterior ray. ~~One~~ Due to the relaxed state of the starfish or some other physiological factor which prevents the lateral arms assuming their usual state of ventro flexion, these droop to the stubstrate and become the "posterior attached arms" (rays c,e in fig. 14). Now the factor, which causes the moving forward of the back rays when the direction of the coordinated impulse, as seen by the activity of the initiating rays causes locomotion in the opposite direction is the same factor, I think, which causes the complex coordination of the deviation reaction. I have presented the evidence which leads me to think that the factor in question has to do with the passive movement of the middle x ray which will be discussed in connection with the fourth type. The impulse spreads to the tube feet of the two unattached rays. The coordination of these is followed by their raising up over the disc and moving toward the initiating rays in the same way and according to the same principles as described above. (types 1 and 2).

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Jennings fifth type is as follows:

(4) 5. All of the rays attach themselves. Now the turning can be accomplished only by the release of certain rays, when the method passes to one of the types already described.

The method of release as I have observed it is of two kinds. (1) The pull of the other parts of the starfish tear loose attached tube feet. These then retract and other tube feet attach but usually not so tightly as those that were first attached. As this continues the tube feet in the region in question either all become retracted and the ray is pulled free of the substrate and swung over in the righting, ~~or~~ (2) the tube feet become oriented in the direction of the pull and righting proceeds according to method three or four with possibly a lifting of the locomotor (released) ray free of the substrate.

Jennings sixth type has already been described in connection with his second type.

Jenning's seventh type is as follows:

"(6) 7. A still more unusual type is seen in the performance of the righting action without attachment of the tube feet of any of the rays. Preyer (1886) and Romanes (1885) have given account of certain ways in which this is sometimes accomplished. The typical method seems for the starfish to raise its disk high standing on the tips of all the five rays, then to swing one or more rays over, or one or more under or both until the body topples over ventral side down. In my own observations, the righting without attaching the tube feet was seen only when these were experimentally prevented from taking hold. The starfish then writhed and squirmed irregularly, taking various the relation of the moving parts of the animal to the substrate and a consequent orientation of the tube feet in the direction of the movement.

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The method of righting, described by Romanes and Preyer seems to be confined to Astropecten and its allies. I have never had access to one of these species and therefore shall regard this highly specialized sand burrowing group as outside the scope of the present paper. The peculiarities of their righting reaction are said (Romanes 1885) to be contingent upon the fact that the tube feet are not equipped with suckers and hence do not attach.

Description of the righting reaction as it occurs when the tube feet are prevented attaching by inverting the animal on sand.

With the animals at my disposal it was thought possible to prevent the attachment of the tube feet# by inverting upon sand.

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The behavior of a large sluggish Pisaster, when inverted on sand is interesting in connection with Moore's (1916, 1918, 1920a 1920b) recent observations on strychnine poisoned starfish. The tube feet at the tips of all of the rays of the large sluggish animals I had under observation extended out toward the tips and the rays bent dorsally, setting themselves more nearly at right angles to the actively extended tube feet. The tube feet however did not attach as they came in contact only with sand. The coordination of tube feet did not spread back very far and the dorso-flexion involved only the distal parts of the rays. For some time all five rays remained dorso-flexed. When the animals were placed on their ventral side on the sand, there was still a very marked tendency for the rays to all bend dorsally at the tips.

Now when a similar specimen, large and sluggish, was placed in a dish of strychnine sulfate in sea water 1-10,000 the same picture appeared, with the additional factor that the tube feet suckers were so paralized that they could not attach to a solid substrate. There was then, a tendency toward dorsoflexion at the tip of the rays and a failure of the coordinated impulse to spread readily among the tube feet as a result either of the paralysis of the tube feet by strychnine and of prevention of their attachment on sand.

These results are probably merely analogous to those of Moore on Asterias forbesi and tend to demonstrate the many ways in which a given response may be brought about in the various representatives of the asteroidea. I have, moreover, so far been unable to get in Pisaster the marked dorso-flexion which Moore figures for Asterias forbesi.

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The behavior of a large sluggish Pisaster when inverted on sand is interesting in connection with Moore (1916, 1918, 1920, 1920a) recent observations on strychnine poisoned starfish. The tube feet at the tips of all of the rays of the large sluggish animals I had under observation extended out toward the tips and the rays bent dorsally, setting themselves more nearly at right angles to the actively extended tube feet. The tube feet however did not attach as they came in contact only with sand. The coordination of tube feet did not spread back very far and the dorso-flexion involved only the distal parts of the rays. For some time all five rays remained dorso-flexed. When the animal ~~was~~ placed on its ventral side on the sand, there was still a very marked tendency for the rays to all bend dorsally at the tips.

Now when a similar specimen, large and sluggish, was placed in a dish of strychnine sulfate in sea water 1-10,000 the same picture appeared, with the additional factor that the tube feet suckers were so paralized that they could not attach to a solid substrate. There was then, a tendency toward dorsoflexion at the tip of the rays and a failure of the coordinated impulse to spread readily among the tube feet as a result either of the paralysis of the tube feet by strychnine and of prevention of their attachment on sand.

These results are probably merely analogous to those of Moore on <u>Asterias forbesi</u> and tend to demonstrate the many ways in which a given response may be brought about in the various ~~xxx~~ representatives of the asteroidea. I have, moreover, so far been unable to get in <u>Pisaster</u> the marked dorso-flexion which Moore figures for <u>Asterias forbesi</u>.

It would be obviously impossible for the suckers to attach, yet the animals (*Asterina* especially) righted themselves quite as neatly as on a solid substrate. *Pisaster*, however, would not right easily unless in active locomotion at the time of inversion.

A specimen actively crawling in the direction of a e (fig. 16) was quickly inverted on sand. The tube feet, which were retracted because the animal was lifted from the substrate, extended at once toward a e. B and d moved up orally and twisted toward a e. C. bent up and over the disk while a & e twisted toward each other and the tube feet, as soon as they came in contact with the sand, began executing the step reflex. Thus each ray moved so as to set itself more nearly at right angles to its actively extended (Oriented) tube feet. The stepping activity of the tube feet on a e resulted in their doubling back under themselves, so that the tube feet were striking out toward the disk instead of away from it (see rays ae fig. 18, 19, 20). The step reflexes of the tube feet in contact with the sand were very active, the ends of the feet ploughing back through the sand and scattering the grains on all sides to a distance of one or two centimeters. The movements thus initiated continued until the rays a e had walked back under the disk and the other rays had moved up over the disk far enough to overbalance the animal and complete the somersault. Locomotion then continued in the direction of a e.

The righting reaction of *Asterina* on sand is even neater than that of *Pisaster*. This is due to the very great flexibility of the ray tips and to the strength and size of the large disked tube feet. The animal rights nearly as quickly and easily as on a solid substrate.

## INTERPRETATION OF THE RIGHTING REACTION AS A PHASE OF LOCOMOTION

### Evidence from the movement of the tube feet and arms.

In general terms, the above interpretation is that the orientated tube feet extend out in the direction of their orientation and in this state are ready to give the step reflex upon contact stimulation. In the absence of such contact stimulation there are reflex connections between the myodermal sheath and the ambulacral nervous system of such a nature that the ray, by twisting or bending or both sets itself more nearly at right angles to the actively oriented tube feet. Fig. 18 illustrates the first movements of an animal inverted during active locomotion toward a e. All of the extended tube feet are protruded in the direction of the former anterior. Figs. 19 and 20 illustrate the movements of the arms as described already (pp 62 ) which result in righting and in the ray assuming a position more nearly at right angles with the oriented tube feet. During the righting process the unstimulated tube feet remain extended toward the animal's anterior. The rays a e, however, in accordance with the above principle, bend toward one another and down so that the tube feet come in contact with the substrate, execute the step reflex and in the manner outlined above initiate the righting.

The tube feet, however, have been regarded (Romanes and Ewart (1881), Preyer (1886), Loeb (1900), Jennings (1907), Moore (1910a; 1910b) Cole (1913a)) as taking hold of the substrate and pulling the animal over. Observation of the reaction as it occurs on sand show that this pulling is not a fundamental or necessary part of righting. Pulling by oriented tube feet is, however, a part of the step reflex. Since attachment increases with the resistance to the step (pp. 19 ff.), and the resistance to the step, in the initiation of the righting reaction, is very great, it follows that attachment is tight and pulling is the most noticable activity of the tube feet. It is this pulling, that has obscured the eyes of observers, the more important and fundamental thing, of which this pulling is merely a part, namely the step reflex.

In general terms, the above interpretation is that the unstimulated tube feet extend out in the direction of their orientation in this state are ready to give the step reflex upon contact stim- tion. In the absence of such contact stimulation there are reflex nections between the myodermal sheath and the ambulacral nervous tem of such a nature that the ray, by twisting or bending or both s itself more nearly at right angles to the actively oriented tube t. Fig. 18 illustrates the first movements of an animal inverted ing active locomotion toward a g. All of the extended tube feet protruded in the direction of the former anterior. Figs. 19 and illustrate the movements of the arms as described already (pp 62 ) result in righting and in the ray assuming a position more nearly right angles with the oriented tube feet. During the righting pro- the unstimulated tube feet remain extended toward the animal's rior. The rays a e, however, in accordance with the above princi- bend toward one another and down so that the tube feet come in tact with the substrate, execute the step reflex and in the manner lined above initiate the righting.

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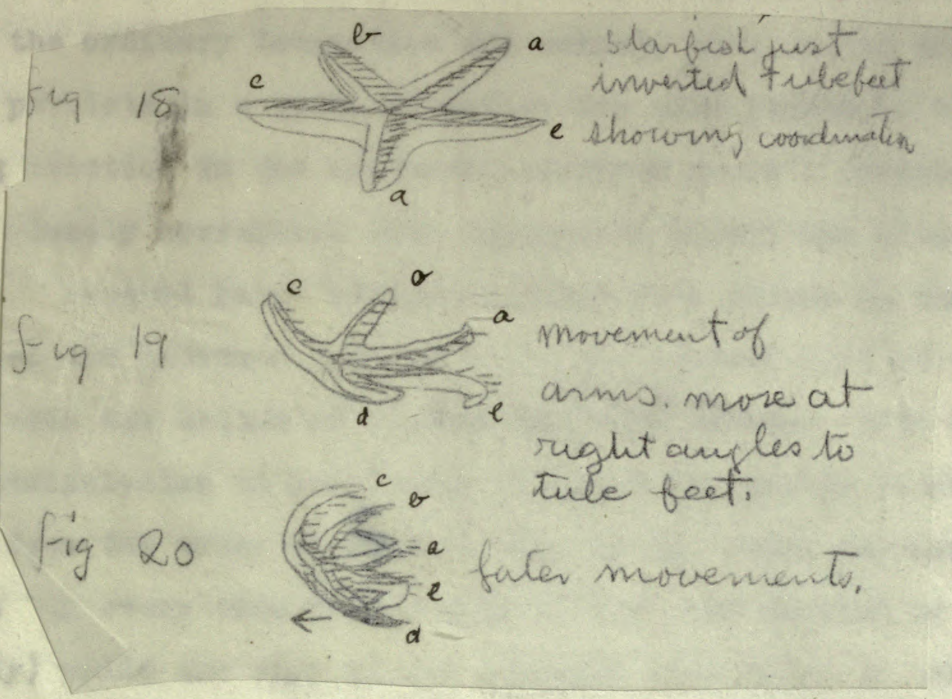
If then the righting movements of the arms are dependent upon the initial stages of the step reflex (oriented tube feet) and the righting movements of the tube feet are slightly modified step reflexes, righting is itself a phase of locomotion.



Evidence from the fact that the stimulation of the dorsal myodermal sheath of the ray is not an essential factorin the righting reaction.

If the righting reaction is simply a modification of ordinary locomotion, it would be expected first that contact stimulations on the dorsal myodermal sheath of the ray do not play an essential part in the ordinary locomotion and second, that, since the locomotor impulse persists in a given direction for some length of time, the righting reaction in the locomotor specimen shows a direction which is very closely correlated with locomotion before and after righting.

Several large active starfish were picked up when in rapid locomotion and balanced inverted with the central part of their disks resting upon the bottom of a small inverted beaker. Care was taken in the manipulation to touch only the disk and not to remove the animals from the water or subject them to any other unnecessary stimulation. In every case two or more of the rays started to bend down (dorsally) while the rays on the opposite side began to bend up. The latter movements were more rapid than the former and the starfish soon overbalanced and fell off the beaker. This was repeated so many times that there is no doubt in my mind that the dorsoflexion and ventroflexion results of the operation of the "unified impulse" persisting from the locomotion. That these movements are homologous with the early righting movements (Jennings type 1) is indicated by the fact that the rays which turn down turn also, usually, toward each other.#

# This conclusion is rendered more probable by the fact that some of the neurotomized starfish when coordinated in locomotion would show righting movements if inverted quickly and gently. These movements were similar in direction to those of the normal animal but were complicated by the fact that sooner or later these animals tended to take the "tulip form". (Romanes and Ewart 1881). In a few cases they righted themselves quite promptly.

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Moore (1920) states that if suspended with the ventral side down, an Asterias forbesi will remain motionless in a state of ventral flexure indefinitely. This while not absolutely true of an active Pisaster especially at first, and very far from true of an active Pycnopodia, may be said to describe the behavior of the more inactive specimens that I have tried the experiment upon. Moore says, furthermore, that if the dorsal wall of a ray of such a suspended specimen be irritated by rubbing it with a glass rod, the ray will flex dorsally. I have confirmed this. Moore, however, neglects to mention a fact, first observed by Romanes and Ewart (1881) that the tube feet of such a ray whose dorsal dermis is irritated increase in activity. The normal orientation of tube feet on an active but unoriented speciman is toward the tip of the ray. It would seem then that the dorsal flexure is due to the principle that a ray tends to set itself more nearly at right angles to the actively oriented tube feet. This is perhaps the more acceptable as a point of view since the activity of the tube feet has been observed to spread to the tube feet of other rays and to be followed by dorsal movements or lateral twistings of these other rays.

Moore comes to the conclusion from these and similar experiments that the dorsal flexures of the rays which he has elicited by contact stimulations are the separate parts of the righting reaction. Aside from the fact that the righting reaction has been observed to start without any contact stimulation of the rays, my observations and the statements available in the literature have led me to the conclusion that lateral twistings of the rays are much more important in the righting reaction (save that of Astropecten) than are mere dorsal flexures.

Evidence from the persistence of the "unified impulse"

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Evidence from the persistence of the "unified impulse"

It remains now to inquire into the correlation between the direction of righting and that of locomotion before and after the reaction. Cole (1913d) has presented some evidence on this point, from which he draws negative conclusions. His analysis of the data is, I think, incomplete and the data are not statistically representative.

He argues as follows.

"In table 4 are shown the results of a number of tests to determine what relation exists between the arms used in righting when the starfish is placed on its aboral surface and the direction of locomotion previous to and subsequent to the righting reaction. The data may be summarized as follows.

| Arms | c | cd | d | de | e | ea | a | ab | b | bc |
|---|---|---|---|---|---|---|---|---|---|---|
| Crawling previous to test | 2 | 6 | 5 | 1 | | | 3 | | 2 | |
| used in righting | | 3 | | | 2 | 16 | | 1 | | 2 |
| crawling subsequently | 2 | 9 | 5 | 1 | | | 2 | | | 3 |

This shows that whereas the four speciments used in these tests righted themselves on arms e a sixteen out of twenty-four times, they had been in nearly all cases crawling in a direction nearly opposed to these arms, and moreover they continued locomotion in the same general direction after righting themselves. An examination of the individual records reveals the same relations in a great majority of cases."

Below is table 4 to which column 2 and column 5 have been added to help in interpreting the data. Cole's studies have led him to the conclusion that the starfish studied crawls with e anterior, more than with any other rays anterior. Unfortunately, however, in these experiments he chose animals that were not typical in this respect, since in no trials were they crawling toward e, and in all but four trials were crawling in a very different direction. This in connection with the fact that only four specimens were used, all presenting an unusual

## -Table 4-

### Relation of arms used in righting to direction of previous and subsequent crawling.

| Individual | Previously crawling anterior | Arms used in righting | Shift of physiological "anterior" (rays) | Subsequently crawled anterior | Shift of anterior from "previously crawling" (rays) |
|---|---|---|---|---|---|
| 14 After trial 50# | d | ea | 1.5 | -- | -- |
| 10 Before " 1# | -- | ea | -- | c | -- |
| 10 After " 10# | a | e(b) | 1 | cd | 2.5 |
| 10 After " 16# | c | e(ab) | 2 | bc | .5 |
| 10 After " 28# | cd | ea | 2 | cd | 0 |
| 10 following day | -- | cd | -- | bc | -- |
| 10 " " | bc | bc | 0 | a | 1.5 |
| 10 " " | a | cd | 2.5 | a d | 2 |
| 12 Trial 1 | -- | bc | -- | a | -- |
| 12 " 2 | a | ea | .5 | de | 1.5 |
| 12 " 3 | de | ea | 1 | ad | 1 |
| 12 " 4 | cd | ab | 2 | c | .5 |
| 12 " 5 | c | ea | 2.5 | cd | .5 |
| 14 " 1 | -- | ea | -- | d | -- |
| 14 " 2 | d | ea | 1.5 | d | 0 |
| 14 " 3 | d | ea | 1.5 | cd | .5 |
| 14 " 4 | cd | ea | 2 | cd | 0 |
| 14 " 5 | cd | ea | 2 | cd | 0 |
| 14 " 6 | cd | ea | 2 | d | .5 |
| 14 " 7 | d | ea | 1.5 | d | 0 |
| 14 " 8 | d | ea | 1.5 | cd | .5 |
| 14 " 9 | cd | cd | 0 | stationary | -- |
| 14 " 10 | -- | ea | -- | bc | -- |
| 14 " 11 | bc | ea | 2 | cd | 1 |
| Average | | | 1.5 | | .7 |

These trials were of a series of 499 showing the persistence of the physiological anterior in a general direction, which tends to rotate slowly to the right or the left.

direction of locomotion, leads me to believe that the data ~~is~~ are not a good foundation for any conclusion. Moreover the conclusion ~~it does~~ they do indicate is not that drawn by Cole.

As seen from an examination of column 5, the 17 records show that the Physiological anterior has shifted in one direction or the other anaverage of seven tenths of an inter radius, per reaction. Coles conclusion on this point, as seen above is that "they (the starfish) continued to crawl, in the same general direction (as they did before) after righting themselves."

Moreover, as seen from an examination of column 3, the 19 records show an average shift of anterior (referring to the rays used to right as anterior) of 1.5 inter radii per reaction. Coles conclusion on this point, however is that the animals right in a direction nearly opposite to that in which they were previously (and subsequently) crawling. But the arithmetical difference between these averages of data (1.5 - .7= .8) is .8 of an interradius a shift which is approximately equal to the shift (.7 interradius) which Cole regards as no shift at all. Obviously, then a detailed examination of Coles data does not confirm his conclusions.

With an idea of clearing up the relationship between the physiological anterior and the arms used in righting seventy-five experiments were made with twenty-six starfish (20 Pisaster and 6 Asterina). The starfish used were in active locomotion, except in case of some of the Asterina as shown in the record. Manipulation was as gentle as possible, the animal being picked up by the disk and inverted quickly without, in most cases, lifting it above the surface of the water. Directive factors in the surroundings such as light or areas of shaddow etc., were excluded by rotating the animal in successive trials.

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Relation of arms used in righting. to direction of previous and subsequent crawling.

| dividual. | Direction before inverting. | Arms first bent down. | Shift of anterior in radii | Arms bent up ventrally. | Arms righted on | Shift of anterior in radii | Direction after righting | Shift of anterio in radii |
|---|---|---|---|---|---|---|---|---|
| umn } | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| .1 Pis - aster | ae | aed | 0.0 | bc | ed | 1.0 | e | 0.5 |
| 2 " | ae | aeb | 0.0 | ed | e | 0.5 | ed | 1.0 |
| 2 " | ae | aeb | 0.0 | bc | ab | 1.0 | ae | 0.0 |
| 1 " | de | e | 0.5 | (a)bcd | (a)e | 1.0 | ae | 1.0 |
| 1 " | e | a(e) | 0.5 | -- | ae | 0.5 | ae | 0.5 |
| 2 " | de | dea | 0.0 | bc | d | 0.5 | cd | 1.0 |
| 4 " | a | (a)bcd | 0.0 | bc | --- | -- | -- | -- |
| 5 " | de | de(c) | 0.0 | bc | de | 0.0 | ae | 1.0 |
| 5 " | e | ae(d) | 0.5 | bc | a(d)e | 0.5 | e | 0.0 |
| ' 5 " | ae | a(b)de | 1.0 | c(b) | de | 1.0 | d | 1.5 |
| ' 5 " | c | bc | 0.5 | a | bc | 0.5 | bc | 0.5 |
| ' 5 " | b | bc | 0.5 | dea | bc | 0.5 | c | 1.0 |
| ' 5 " | ae | eda | 1.0 | bc(d) | ae | 0.0 | ae | 0.0 |
| ' 7 " | e | ae | 0.5 | bcd | ea | 0.5 | ea | 0.5 |
| ' 8 " | bc | (b)c(a)d | 0.0 | (b)[illegible] | bd | 1.0 | cd | 1.0 |
| ' 8 " | de | de | 0.0 | -- | de | 0.0 | d | 0.5 |
| ' 7 " | cd | b | 1.5 | acde | b | 1.5 | b | 1.5 |
| ' 5 " | de | de(c) | 0.0 | bca | de | 0.0 | de | 0.0 |
| ' 7 " | ae | e(a)b | 0.0 | (b)cd | ae | 0.0 | ae | 0.0 |
| ' 5 " | a | (b)ae | 0.5 | bc | ae | 0.5 | -- | -- |
| ' 9 " | ae | abcd(e) | -- | e | ab | 2.0 | stopped | -- |
| ' 9 " | de | (a)dc | 1.0 | ebc | d c | 1.0 | ae | 1.0 |
| ' 10 " | bc | bc(a) | 0.0 | -- | -- | --- | -- | -- |
| ' 11 " | bc | bc | 0.0 | ade | bc | 0.0 | bc | 0.0 |
| ' 7 " | cd | cd | 0.0 | abe | cd | 0.0 | -- | -- |
| 12 " | de | (a)ed | 0.0 | bc | ed | 0.0 | ed | 0.0 |
| 13 " | e | (eabcd) | 0.0 | (abcde) | -- | -- | -- | -- |
| 12 " | cd | dec | 1.0 | ab | de | 1.0 | de | 1.0 |
| 12 " | de | (a)de | 0.0 | bc | ae | 1.0 | e | 0.5 |
| 12 " | de | e(ad)a | 1.0 | bcd | ea | 1.0 | ea | 1.0 |
| 12 " | ea | ed | 1.0 | ab | ed | 1.0 | ed | 1.0 |
| 14 " | c | d c | 0.5 | aed | dc | 0.5 | c | 0.0 |
| 15 " | c | (c) | 0.0 | tulip form | -- | -- | -- | -- |
| 16 " | cd | a | 2.5 | (e)(a)bcd | ae | 2.0 | ae | 2.0 |
| 16 " | ae | ae | 0.0 | bcd | ae | 0.0 | ae | 0.0 |
| 16 " | ae | ed | 1.0 | cba | ed | 1.0 | bc | 2.0 |
| 16 " | ab | ae | 1.0 | cd(e)b | ae | 1.0 | ae | 1.0 |
| 16 " | ae | ac | 0.0 | bcd | ae | 0.0 | ae | 0.0 |
| 17 " | bc | bc | 0.0 | aed | bc | 0.0 | bc | 0.0 |
| 17 " | bc | bc | 0.0 | aed | bc | 0.0 | bc | 0.0 |
| 17 " | bc | bc | 0.0 | aed | bc | 0.0 | bc | 0.0 |
| 18 " | cd | bc | 1.0 | aed | bc | 1.0 | cd | 0.0 |
| 19 " | d | abcde | -- | (dea) | bc | 1.5 | cd | 0.0 5 |
| 19 " | cd | abcde | -- | e | bc | 1.0 | (b)cd | 1.0 |
| 19 " | cd | abcd(e) | -- | e | bc | 1.0 | c | 0.5 |

| | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|---|---|
| 46 | No.20 | Aster-ina | ae | ae(b) | 0.0 | dcb | ae | 0.0 | stopped | -- |
| 47 | " 20 | " | ab | ae(b) | 1.0 | abc | ae | 1.0 | ab | 0.0 |
| 48 | " 20 | " | de | (de)abc | 0.0 | ac(b) | de | 0.0 | de | 0.0 |
| 49 | " 20 | " | ae | ae | 0.0 | bcd | ae | 0.0 | ae | 0.0 |
| 50 | " 20 | " | c | c | 0.0 | abcd | c | 0.0 | stopped | -- |
| 51 | " 20 | " | ea | ea(bc) | 0.0 | dbc | ea | 0.0 | ea | 0.0 |
| 52 | " 20 | " | de | (d)ea | 0.0 | bcd | ea | 1.0 | cd | 1.0 |
| 53 | " 20 | " | c | c | 0.0 | tulip form | | -- | -- | -- |
| 54 | " 20 | " | d | d | 0.0 | (de) | de | 0.5 | stopped | -- |
| 55 | " 21 | " | ae | ae | 0.0 | -- | cd | 2.0 | de | 1.0 |
| 56 | " 22 | " | bc | bc | 0.0 | aed | bc | 0.0 | stopped | -- |
| 57 | " 21 | " | de | abcde | stopped | | -- | -- | -- | -- |
| 58 | " 23 | " | ae | ae | 0.0 | stopped | | -- | -- | -- |
| 59 | " 23 | " | a | a(e) | 0.0 | bcd | ae | 0.5 | stopped | -- |
| 60 | " 24 | " | 0(sta) | abcde | stopped | | -- | -- | -- | -- |
| 61 | " 24 | " | de | ba | tulip form | | -- | -- | -- | -- |
| 62 | " 24 | " | de | bc | 2.0 | ade | bc | 2.0 | stopped | -- |
| 63 | " 25 | " | bc | bc | 0.0 | ade | bc | 0.0 | stopped | -- |
| 64 | " 25 | " | ab | ae | 1.0 | bcd | ae | 1.0 | " | -- |
| 65 | " 25 | " | bc | bc | 0.0 | ade | bc | 0.0 | " | -- |
| 66 | " 25 | " | ae | ae | 0.0 | bcd | ae | 0.0 | " | -- |
| 67 | " 26 | " | ab | ae | 1.0 | bcd | ae | 1.0 | " | -- |
| 68 | " 26 | " | de | eacd | 1.0 | bm | e | 0.5 | " | -- |
| 69 | " 23 | " | e | de | 0.5 | dcb | ae | 0.5 | " | -- |
| 70 | " 22 | " | de | de | 0.0 | cab | de | 0.0 | " | -- |
| 71 | " 23 | " | ab | ae | 1.0 | cdb | ae | 1.0 | " | -- |
| 72 | " 25 | " | 0Stationary | | | rigid | | tulip form | | |
| 73 | " 24 | " | " | " | | " | | " | " | |
| 74 | " 25 | " | " | " | | " | | " | " | |
| 75 | " 24 | " | " | " | | " | | " | " | |
| Average | | | | | .38 (64 trials) | | | .6 (62 trials) | | .57 (44 trials) |

Records were taken (column 1.) of the direction of locomotion before righting and (column 2) the arms that, after inverting, the animal, first twisted and bent down toward the substrate. These two findings were compared in each experiment and the shift in either direction of the leading rays or "physiological anterior" set down in column 3. The turning down of certain rays is usually followed ( xxxx or preceded ) by a lifting up of others. The rays that lifted up free of the substrate - but not those that were oriented on the substrate, in the way described above, to walk over the initiating rays, were next recorded (column 4).

The rays that turned down were not, always, of course the same as those that the animal uses in righting. These latter are listed in column 5, and the shift of anterior from the direction before inverting to the arms used in righting is listed in column six. The anterior after righting is listed in column 7 and its shift from the direction before inverting is listed in column 8. Thus the shifts of anterior, listed in columns 3,6 and 8 refer to the original anterior before inverting.

A comparison of the averages obtained here, and those drawn from Cole's data shows that careful manipulation of the starfish and the use of a large number of individuals reduces the shift of anterior considerably. As shown by the rays that are first turned down, the anterior at the beginning of righting has shifted .38 of an inter-radius on an average of 64 observations. As shown by the rays on which the animal rights, the anterior during the righting reaction has shifted .6 of an inter-radius from where it was before the animal was inverted. After righting, the anterior shifts slightly <u>back toward</u> its original direction, as shown by the fact that the average shift after righting is less than during righting. This shows more markedly in the average

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This return of the anterior toward its original direction is an example of the tendency which we have noticed in connection with the deviation reaction ( p. 57 ) for the coordinated impulse to return to its original direction, even after having been actively oriented in some other direction.

Cole (1913) has shown very conclusively that the impulse to locomote, in the starfish tends ~~thus~~ to maintain the same general direction, from trial to trial.(Between each trial the animal was held inverted by the disk until the rays dropped and then "started" on the bottom of an aquarium in a non-directive chamber.). The tendency to keep in the same direction was of course only general, as there was also a rotation of the anterior toward the right or toward the left, and certain aberrant deviations, of from one half to two and a half inter-radii occurring quite frequently. In x ~~computing~~ counting up these deviations from the table opposite p. 16 (Cole) it was found that they amounted to a sum total of 217 inter-radii in 499 trials. This amounts to a shift of anterior of .43 inter-radii per trial which is quite comparable quantitatively with the figures (.38 ,.60,.57) inter-radii)obtained from the status of the direction of the coordinated impulse throughout the righting reaction.

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## SUMMARY

1/ Pisaster ocraceus presents the three following well marked physiological states (1) "Rigid" (2) "locomotor" (3) "active but unoriented" The responses of the tube feet and arms differ markedly according to the physiological state of the animal Other starfish studied present analogous states.

2/ Extension of the tube feet depends upon the proper physiological state and absence of stimuli which cause retraction. An isolated tube foot, inflated with water under pressure can be caused to slowly extend but not quite normally.

3/ Attaching is conditioned by the proper physiological state. An isolated tube foot, properly prepared and inflated with water is more apt to attach if taken from a rigid starfish than from a locomotor starfish. Attaching may involve only a part of the ambulacral disk.

4/ Withdrawal is a response to contact stimulation, as is detaching, under certain conditions.

5/ The step reflex intergrades with the withdrawal response as elicited by contact stimulation of the ambulacral disk. It is dependent upon contact stimulation and the presence of the locomotor impulse, which orients the step reflex and conditions the tube foot to be rigid and support animal during locomotion. The tube foot is attached most strongly during the first part of the step reflex. The tube foot is attached with 2.8 (Asterina) or 2.06 (Pycnopodia) times as much force as it exerts in pulling against resistance. The factor is relatively constant for various values of the resistance. The strength of the step reflex varies markedly with different species.

6/ Coordination of the tube feet of the rigid starfish, like that of the gills, is a simple spread of extension or retraction. It is referable hypothetically to a simple nerve net.

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6/ Coordination of the tube feet of the rigid starfish, like that of the gills, is a simple spread of extension or retraction. It is referable hypothetically to a simple nerve net.

7/ Coordination in the active but unoriented starfish involves orientation of the distal tube feet, toward the tips of the rays. With the rays on separate substrates, this tendency results in their walking in five different directions. Under pathological conditions this tendency results in autotomy. Orientation of the tube feet is not referable to a simple nerve net as is coordination in extension and retraction but to a more complicated and possibly an independent mechanism.

8/ The unified impulse is formed in three ways: (1) by the spreading back of the oriented state in the tip of one of the rays. Various factors may cause the relative increase which results in its spread over the rest of the animal (2) by the spreading back and fusion of the oriented states in adjacent rays. (3) By direct orientation of the tube feet from exitation of the dermal nerve net or the tube feet, themselves.

9/ Behavior of the oriented animal is conditioned by all of the above factors acting at the same time and in nice balance against each other. In the actively migrating starfish the tube feet are all oriented in the same direction. ?

10/ The unified impulse, (1) in some types of righting reaction, (2) in the deviation reaction, (3) in the locomotor starfish with a curved lateral arm, is broken up into areas in which the tube feet are oriented in different directions. This is highly adaptive. A possible physiological explanation is seen in the traction on the tube feet resulting from the movement of the rays over the substrate. Evidence for this hypothesis is drawn from (1) Neurotomized starfish (2) starfish with the rays placed on separate substrates; (3) the mechanics of the deviation reaction.

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11/ The righting reaction is a phase of ordinary locomotion with the starfish in more or less a state of unified coordination The movements of the arms are explained on the assumption of reflex connections by which the arms are bent or twisted more nearly at right angles to the actively oriented tube feet. Evidence for this conclusion is drawn (1) from the movements of the tube feet and arms: (2) from an analysis of the reaction when the tube feet are prevented from attaching by inverting the animal on sand; (3) from the fact that stimulation of the dorsal myodermal sheath of the ray is not an essential factor in the righting reaction (4) from the fact that the "unified impulse" persists during the righting reaction in the same direction to a degree quantitatively comparable to its persistence in ordinary locomotion (Cole).

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