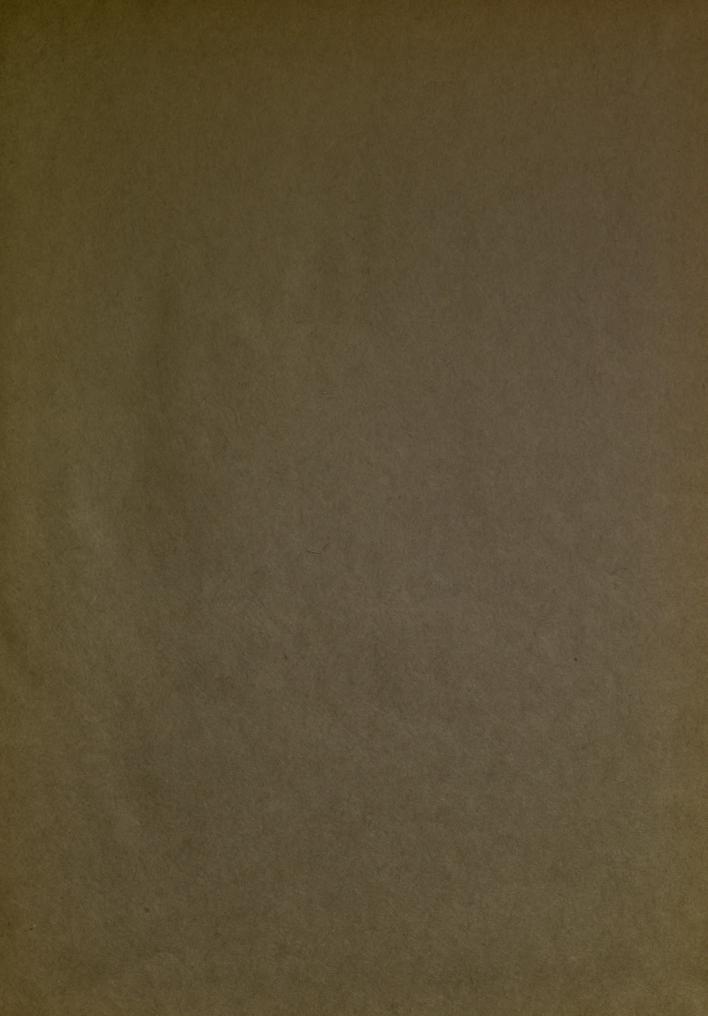
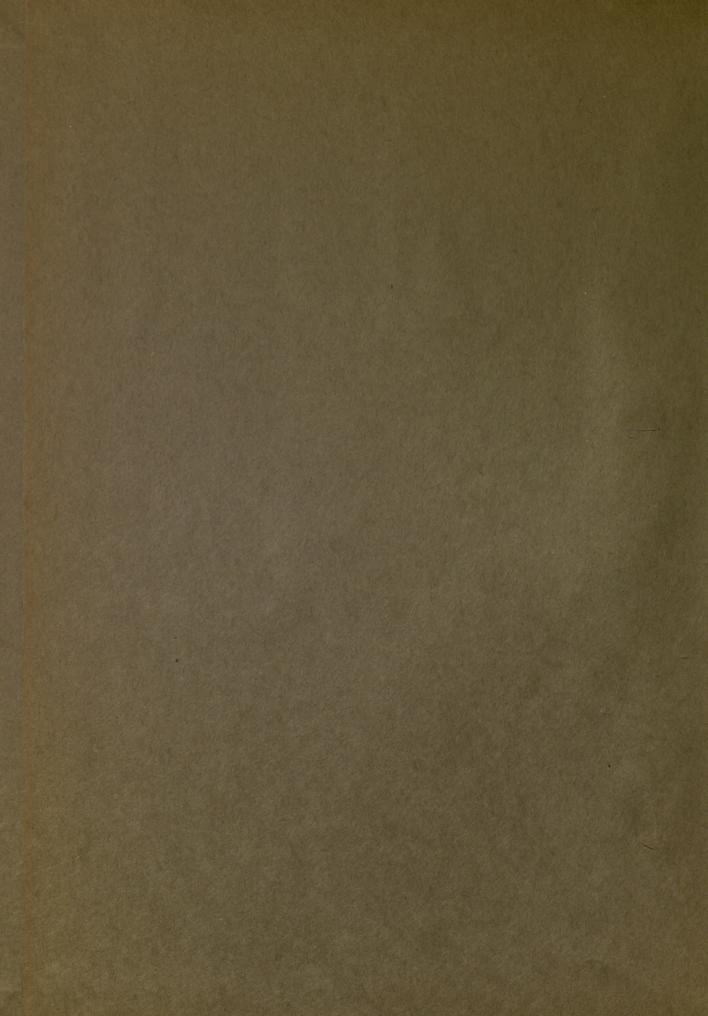
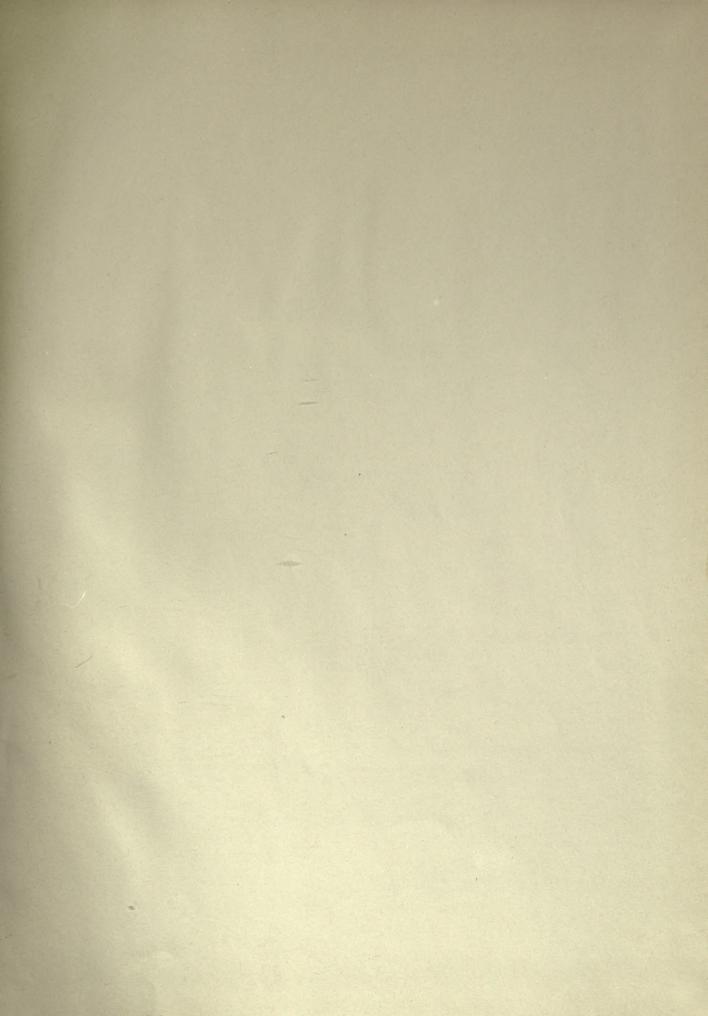
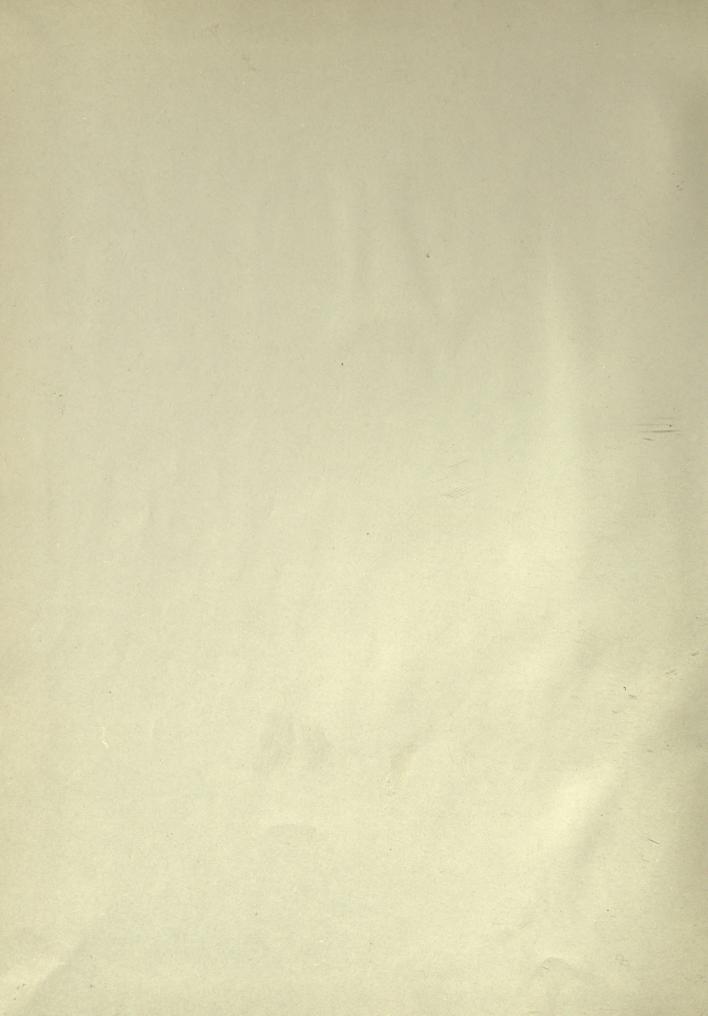


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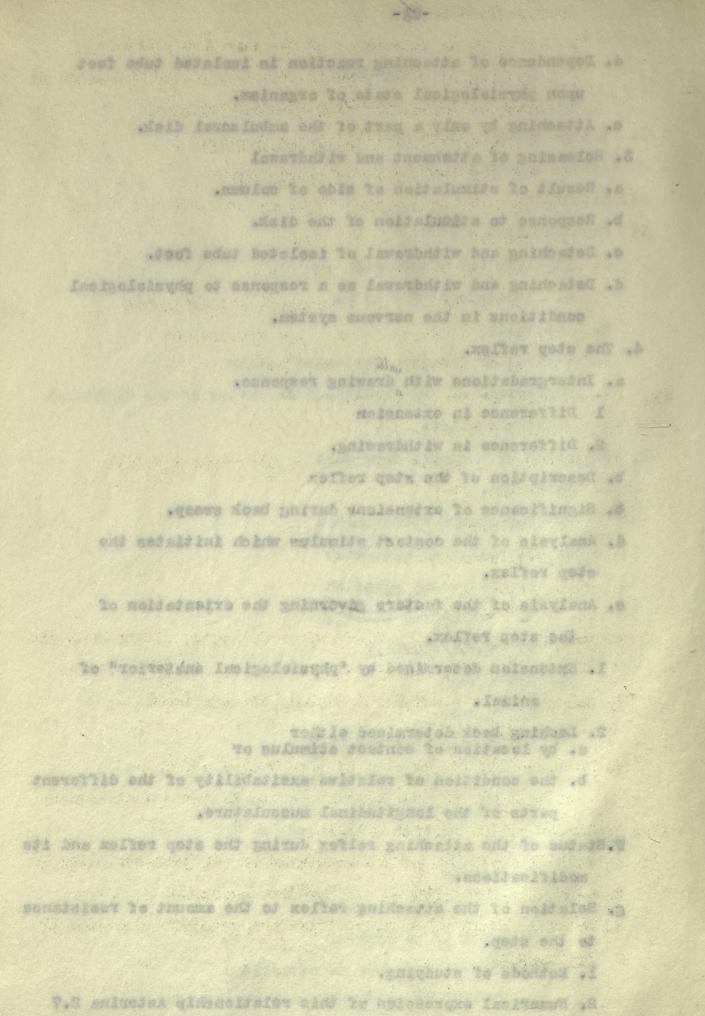
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INTRODUCTION

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.

ACINOWLEDGEKENTS

I wish here to express my thanks to Prefessor 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 Professoro S. S. Maxwell and T. C. Burnett, of the Physiology department of the University of California for their helpful advice.

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MATERIALS.

The following starfish were studied intensively: <u>Pisaster ochraceus</u> (Brandt) <u>Pycnopodia helianthoides</u> (Stimpson) <u>Asterina miniata</u> (Brandt)

Supplementary observations were made on the following echinoderms:

Leptasterias equalis (Stimpson) <u>Pisaster brevispinus</u> (Stimpson) <u>Evasterias troschelii</u> (Stimpson) <u>Strongyogentrotus franciscanus</u> (Agassiz)

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

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

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PHYSIOLOGICAL STATES

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<u>Plaster ograceus</u>, 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

To my wife, for her many anearful exertifiess and her willag help in numerous ways, is due my fullest gratifude.

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A remarkable difference was evident in the physiclety

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 <u>Pisaster ocraceus</u> taken from Cakland 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"

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(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 (19086), Bohn (1908), Cowles (1911:), 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.

<u>Pycnopodia helianthoides the large 20 rayed "sun star"</u> present these same physiological states in quite as marked a manner as <u>Pisaster</u>. I have never observed <u>Pycnopodia</u> 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

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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 clear, although in the unoriented state one often sees the animal make lurches, as if the crawl in this and then in that direction without actually doing so.

The other starfish observed seem to present different physiclogical 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 physiclogical state of the animal: (1) extension, (2) attaching,(3) withdrawal, (4) step reflex.

EXTENSION

Conditions of extension

(1) 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 and, 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 ex 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 initiatian tube feet of such a starfish and those of a normally active one is that the former are not away directed out 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.

source Mechanismo mel correcture Loward the persistance and canal,

The mechanism of extension, first described by Reamur (1910) 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 out 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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The extension is conditioned in direction by the foremetor activity of the enteril as a whole. If the exarting the educating in the the direction of a cortain are, for instance, the twist feet will, is the absence of context stimulation extend themesive is this direction, and remain to extended would extend to afther to retract or execute the star reflect educe to retract or execute the star reflect.

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In the abstitution of an erigid starties the the fort of the suber part of the say are, in the epsence of manadt simulation, extended sore or lass toward the tip of the ray and on moving ("feeling") about in the bid direction. This of course is not constant and is more methodole in the active specimens.

extend the hold fort recence on to individuals of the active non-longenets type. The modificitiedable difference betweed the benevior of the boundaries subs feet of such a starfish and there of a personally applied one is that the former are not directed sub from the tige of the reg. They my be writed about approximately at right angles to the reg or avec directed accords toberd the owner.

and it are all a set

The mediantes of extension, three described by Remark (1910) in a very interesting paper to well known. It involves a contraction of the ambulactual angults and a relaxation of the longitudical suscentature of the tube from. To accortain the dependence of this relevantion of the fongitudinal marculature on the redial nervous system, tube feet were out off and tied on to the end of a capillary glass tube. This was concerted with

increased or decreased by raising or lowering a reservoir, which was connected to the capillary tube by a long rubber tube. If the tube feet were injected with water at a pressure of 10 cm (H2O) they would slowly extend in the absence of contact stimulation but not to their whole normal length. The extension was much slower than the active extension of a normal tube foot and not so complete. If caused to contract and then injected with a pressure of more than 2 m (H2O) the extension was not appreciably accellerated but could be made more complete. Tube feet anaesthetized in Mg SO, would extend completely under low pressures. This anaesthetization involved, also relaxation of the circular muscles so that the tube foot presented a noticeably greater diameter than the normal tube foot. In the extended as well as the contracted tube feet there was a quite constant curvature in the direction of a clear longitudinal along the side line up the shaft of the pedicel which I take to be the annance pseudohaemal canal (Cuenot 1888) This curvature persists in the anaesthetized (or dead) pedicel and is therefore probably due to mechanical rather than to physiological factors.

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the organism. The tube feet of Pleaster in ordinary locenstics to

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 hense physiological in its nature and is perhaps analagous to the behavior of a sea-urchin's spine when bent over to one side/ (Von Uexkutll 1900-).

Attaching

Attaching is conditioned by the physiological state of

inition righteners a gaineval to patalat at homeraphics for any and was connected to the availings take by a long rubber table. If this take for any inches inthe destinant with a presente of 10 an (B.O) they would aloudy actual in the avanue of control noisnestne any antiput forman afain winds as see and unksafir is adul Imeron a to noinnoite eviços aut onde memole chos ass took and not to complete. If ounced to constant and thinks notenegro and (Oph) a Start arne to summaring a Male betables .ofelmine even shaw ad blues and beautolleess visioning for and while fort anashetted in Mr. 30, would extend completely maker low presenter. Into anserbactration involved, also releastich a hosticaetti Jool edur enil intil os valtenim veluorio entrate an ited with the set of the set of the set of the set of the the alling a man storil fort subs horsering bet as ilow as bennering The she burge turne in the virentian of a class incard and otens the eide concerns and so of the reacted within I take to be the offerents na sinkaran onne (Jumpe 1830) - This ourvashing porestant Widedway prototonic of the feelbed (boub we) bestronteene on due to peolenioi. rother than to physiological factors, Antipa tabe for pressent and and allowed to ustand aut second deception for the start the particulation of the particular and then were bent clowly and ready in some stand ever had but they whowed a tendency to react bout in thet direction ond the state to bend basis is the original length of given anoss mattaine or a deal tube fool door not think to this bally bally it to nones physicisty and in its as between and is gamman a Analage to the behavior of a sea anothin's spine the bind aver to and alds. (Von Deminist 100063.

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Attaching is conditioned by the physicistical since 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.

\$Structures involved in attaching.

Attaching is a reflex which, though it may be modified by outside factors, involves necessarily only the muscular and nervous structures of the pedicel.

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Tube foot preparations were made as above from actively attaching starfish, great care being exercised to quickly and gently. It was found upon placing such a tube foot against a stubstrate 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 this capable of usinghnumis. Thus they are not infinenced trials.

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

only in bring in such a state of physiclouis=1 activity that the

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 organizes. The tube feet of <u>Pleaster</u> is ordinary locomotion do not attach very strongly. When is the rigid appressed state, however, they are so tightly adherent that sain may be pulled off before the animal can be removed from the substate.

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Mr. Vermonin of the physiological department of Stanford University informs as that he had releaned the tube feet of such a startich one by one with a modile until there were just shough tube feet adhering to suspend the animal from the lever surface of a giaza piete. The bitumsted brok of the disks of these tube feet mainifield by atmospheric pressure was approximately equal to the raight of the startish the subwind that these origins are medicalanified by atmospheric pressure was approximately equal to the saily quite efficient.

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Attaching to a relier which, though it any be modified by consider factors, involves merceberally only the massular and merrous structures of the period. These foot properations were have able as show from actively attaching startlish, processes being shorteled to quickly and genely. It was found upon placing shorteled to quickly and attacts that the abort five opease out of ten, it would attach and not age analy of the disk! This power of ten, it would attach and not trials. interior attacts is abort five opease out of ten, it would attach and not age and to disk). This power of actioning was lost after a for trials. interior of the disk). This power of actioning was lost after a for trials. interior at the foot properetions were also hade from abort the disk the foot properetions were also hade from abort the disk the foot properetions were also hade from abort the disk to be foot properetions were also hade from abort the disk to be foot properetions were also hade from abort the disk to be foot properetions were also hade from abort the disk the foot properetions were also hade from abort the disk to be foot properetions were also hade from abort the disk the foot properetions were also hade from abort the disk and the disk the foot properetions were also hade from abort the disk and and the disk and disk and the disk and the disk and the disk and the di

were not stisching (in active locomotion, feeling shout the sufface

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 the it be unconnected with the radial nervous system (see also Botazzi 1898 and Russo 1913).

It is well known, also, that some times a 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 (Mangold 1909b) theory has not been very widely accepted, 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 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 much a tube foot may restach even the it be upconnected with

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the radial nervous system (see also Rotazzi 1898 and Russo 1913). It is wall known, also, that some times a k starfish is very prome to attach its tube foot tightly to the substrate while at other times the animal's energy is taken up with ideamotion or some other setivity that does not entail tight attachment of the tube feat (Jennings 1907). The experiment shows also that there is a difference is the behavior of the isolated tube feet which corresponds to the fluctuation of the attaching resolution of an animal from time to the According to the staching resolution of an animal from time to the seturity is an attaching to be feet which corresponde to the fluctuation of the attaching resolution of an animal from time to time.

the to "Tomas" which is necepherisally referred to as a fluid. Hat is carried to the muscle through the nerves. Furthermore (1903) by outting the serve which has supplied this toma, the "fluid" may be entrapped in the muscle, and the muscle remain contracted. While this Wrongeld in the messio, and the muscle remain contracted. While this brapped is the new very widely socooted, some of its nepsote are worthy congruent with the behavior of isolates tube feet.

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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 ambulaoral 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

of tube feet so that strument was hook-shap 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.

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ditions which will be

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

Relaasing 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 eligites. It would seem, then, from the difference in behavior of table feet teles from unicals in different physiclological states the this state of specialized irrittebility is a condition of the ambulaced disk and while segendered, must probably, by influences procesting from the reddal serious system, is not dependent upon the system for a rether limited continuance.

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Attaching av only 6 much of the publicants, data. The otherwides rollos does not necessarily invites all of the univelaced disk. The and of a small rod was placed on various party of the lower muchas of a large battrony attaching pediect. The part is control with the end of the rob schooled with grant force, much the disk out of schoole with the red of the rob schooled with grant force, of the disk out of shape, a fine heat and held flat disting a portion of the disk out of shape, a fine heat and held flat disting the disk

The disk as an attaching anoharise, then, doen not not as a whole (Preyer 1886), but rather the incourting endure toward the peater of any property stimulated area.

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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 starfich. 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

The first description that I am find of the step-reflex"

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is that given by Reanur (1714, After describing the surple " Region connection of the annulies ("ting year! like" bulls) and the "lage" (tube feet) he goes on to may "But one byings out

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that are closely analagous. If a starfish is tightly stached 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 ally under the starfish. Buts stimulation sauses the release of the stimulated tube feet and sometimes the release of foighboring tube feet.

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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 an 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.

take up later a more THE STEP REFLEX of the sucches of the sheetles of the state of

Intergradation with withdrawing response.

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

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 conception with the stop reflex, a slight extension constitues countries due probably to an increment transfer of the angular member. Next, in expenses in the num-longentration and the relevant of of later the two for and a beam equent working of the place of collater back the say, this does not interive release of the outbilities by the dire column and the release of stimulation of the outbilities by the the column and the relevant of the relevant of the substrate by the the solution and the release of the substrate by the dire column and the release of the substrate by the the column and the released of stimulation of the substrate start is involved the the scalar directed of the substrate start hereis and the theorem and the start does not the substrate start hereis and the the scalar directed of the schedules

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The first decemption bias I can find of bis"step-teiler is that gives by Loomis (IVI), first describited the service legical connection of the enculias ("siny carf line" balls") and the "logs" (the feet? he goes on to may "Unit one stings out the whole ingenieue hechemies of it when one present thege time, the 'leg' which corresponds to it becomes inflated and clongated. Finally it is seen that on cessation of the pressure the balls refill and the legs become empty and shorten themselves, and it is nothing more than this that the starfish does in extending its legsto press upon the balls, as one may do at any time with his finger. It is easy to imagine a thousand ways in which the starfish can do this. The compressed balls discharge their water into the legs which they inflate and thus extend, but when the starfish ceases to press on the balls, the natural elasticity of the legs, which is considerable causes them to shorten. These legs, thus elongated the animal uses in locomotion by Analysian extending them out toward the body to which the animal wishes to move and attaching to it at a very acute angle. The strength with which the leg remains affixed to this body while trying to make a right angle with this same surface obliges the animal to approach."

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 integrates 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.

the flagt which corresponds to it becomes inflated and Clongs -. Curka ted. Finally it is seen that on essention of the presence the balls refill and the legs become empty and shorten themselves, and it is "eyel ath anthen this the startish does in ortending the lageto press upon the balls, as one may do at any time with his finger. It is easy to imagine a thousand ways in which the starfish can do The compressed balls discharge their water into the lage which . minis they inflate and thus accoud, but when the starfish daugas to press another the natural alasticity of the legs, which is doneider. able causes than to chorten. Iness logs, thus clougated the animal uses in locomption by AAAAAAA extending them out toward the body to since they a is it of gainosita bas even of sedely landse est doldy The strangth with which the leg ramains affind to this body . OINTR segulo secture care and doir signs that a size of galves allies ". desorant to approach edd

of the withdrawing reflex as a response to control stimulation of the disk. The intergrading staps depend upon the presence to a gradier or less degree of a locomotor tendency. This expresses iteally in the inverted or suspended startion, as already shown by an orientation of the extended tube from in the direction of the physiological anterior. If the locomotor impulse is not very strong, the only modifiestion perhaps that will be observable in the vithdrawing resetion, will be an exagention of the tendency to extend after the control stimulation and before the vitheral.

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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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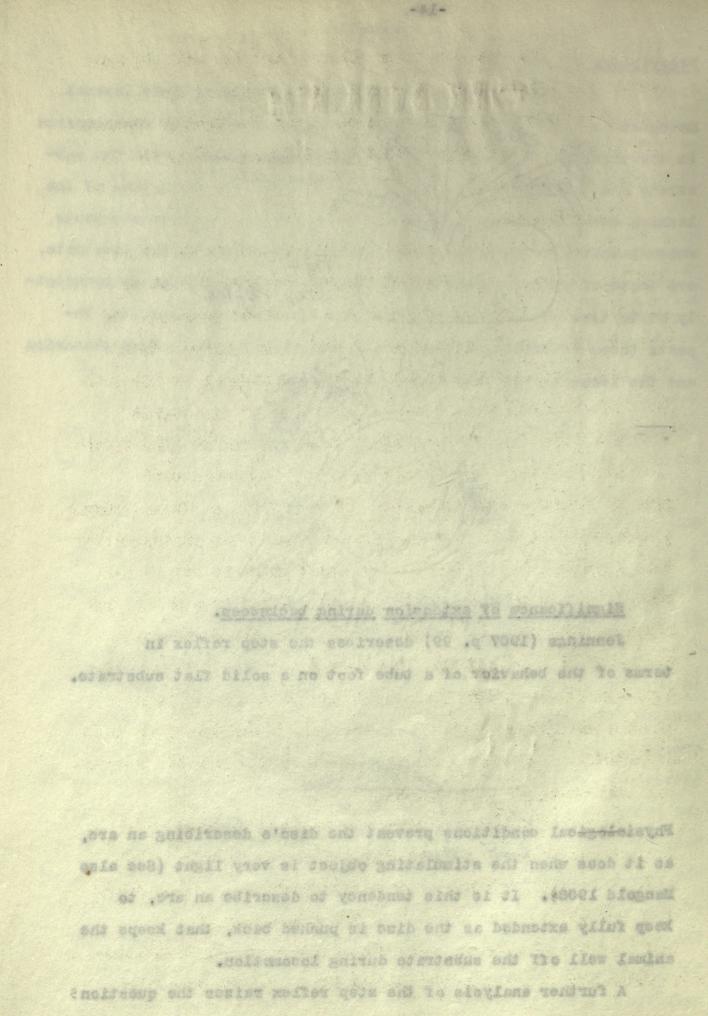
Deder ordinary sireussianses of locamption, this lateral movement is followed by retraction and the retraction by re-extension in the direction of locamption. This involves contact with the substrate and the stimulations which dive rise to the repetition of the leading back, the retraction and the re-extension. These movements which involve, as shown in detail later, situatment to the substrate, are those of ordinary locamption, later to the is the substrate, by as to these movements is bernony with its fellows as to direction, reposts these movements is long as contect stimuli result from extension and the locemetor impulse result unimpaired.

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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 question \$



 (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.

surface film of the water, or these

The stimulus

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The stimulus which sets off the step reflex is one of gentle contact on the disc bontact 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 stepp 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 olear 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 <u>Pycnopodia</u> with the ventral side exposed to the air, presents the likeness of some strange sort of military activity. With maching like regularity the 22,000 bright yellow tube feet

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(1) What is the atimalies which note if off? (2) what factors govern its arientellou?
 (2) What is arientellou?
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 (4) What is the relative etrangic of the step reflex in different species.

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Shen a starfish in active locanotion is brownt above the surface of the writer the step reflex was each to count without further stimulus. An active apoplant of <u>Francodia</u> with the ventral side arguest to the sit, presents the likeness of some strange sort of military activity. With maching like regularity the Se 200 pright relies tube fact ex tend themselves out toward the temporary anterior and then lash back vigorously in the opposite direction, exactly parallel with each other.

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 refles.

That factors govern the orientation of the step reflex? 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 analyzed 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- the most always - to touch the substrate first with the pot-

expected that exitation to contract on the column 1-3 and cause 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

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ex tend in manipule out toward the bemourary apterior and then Lash back signmunity in the procelts direction, eractly parallel aign back back other.

The orne electricities of this is seen if the two two for of a part of much a starfield be subserved. Then only these tube feet that touch the surface film of the witer, or these estimaty exposed to the sir execute the step reflex. The subserved take feet remain pointed in the direction of the tamporary autorior wall uses contact stimulation, from the surface film or fram some sails object initiation the stop reflee.

The first phase of the received, the entension of the time first phase of the received, the entension of the two first phase of the received, the entension of the two for fort fort fort fort of the first phase of the the statement of the entries of the time the statement of the entries of the time the statement of the statement

expected that emilestion to domicrat drawed by his context stimulue might spreed to the side of the foirers 1-5 and cause its contraction more guickly then to the side 5-4. Northermore

reflex with as much readiness and regularity (Pisaster) as a similar stimulus at the place 1. It must be remembered hewever 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 Uexku#11'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.

Status of the attaching reflex during the step reflex. 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 of 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 likelyhood of release (or slipping) is found gradually to encrease during the last phase of the step reflex.

A large grain of sand was placed on one of the ambulacral discs of an active P<u>yonopodia</u>. The step reflex which resulted was so violent that the grain of sand was thrown as from a

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reflex with as much readiness and regularity (Figenbor) as a similar stimite at the place 1. It must be femenbored however that in normal loometion the died is diten placed fist on the substrate, ad that then the tube fact are expected to the sir the surface tension fills may be expected to contract with equal pressure on all sides of the disc, and thus to stimulate then all equally. We make to count then upon the greater excitability of the muscles on the side 1-3 in the post-contact place of the step reflex. This is comparable to the increased tension of the duscley as the side 2-4 in the pre-annials stage of the step reflex. The casilin tions of the tube feet may be explained in terms of Von Denkin I's law of "tonus" or may be lot's moniplained. She that is, of courses where they nove had and forch in the step-reflex with constend erajost off and areains orienterion. The fathers that ont do moles of life instite of the animal will be taken up in connection will an analysis of conrection ties when the bube feet. Status of the straching rolles during his star reller. The attempts of attachment during the stop ration differe anyone and holy bas solvers thereille and this sas lists or as of resistance there is the squartingent of the story In general we may mounted from observations of ordinary lecomo tion that the tendency to attack is strongest, during the programs of the story refler, junt after the backrot. The tube fort cousily remains a that during the first half of the (anicalle to) section to beediently end and methods busying . is found gradually to wareage during the last place of the .mailer gols

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A large grain of same was placed on one of the reculated discs of an active F<u>umprodig</u>. The stap wellow which reculted was so visiont that the grain of much 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 <u>Pisaster</u>, <u>Asterina</u> 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 Astering was tied by a long thread to a spring recorder which was cal/ibrated to grams and set to writke 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:

it is the figstigned by the starfish as it walks against the resistance of the spring. At 2 the glass plate was slid

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ministrure estaguit, a distance of four or five on. (n repeating this, the alevation or "addle of fire" was agen to be such as would entail release of the grain from the dise during the third quarter of the are that the dise describes in lashing back. Venally, however, in <u>Pleaster, Asterim</u> etc. the violence of the lashing back is not as great, and the release is not very sudden or prompt as that such a catapulting action is not often seen in these forms.

Relation of the stration reflex to the amount of

The relation of the attaching reflex to the amount of restatance to the stop was obtained in the following manner: the of the mays of an <u>Astaching</u> was block by a long thread to write on a slowly moving dram. More the animal pulled attack the entries, the strangth of the pull was recorded as animal had pulled the surve shows the mass line. For when the states in the strain of the surve shows the mass line. For when the animal had pulled the surve shows the mass line. For when the dension on the startich we will be resulted in an increase the testing to the surve shows the mass line. For when the states in a startich we will be and the states line of the testing the startich when the mass line of the states is the testing the startich when the states line of the states is the testing the startich and the set states line of the states is the testing to the startich when the states line of the states is the testing to the startich the states line of the states is related in the testing testing when the startes of the states is related in the testing testing the startich to a survey for the testing testing testing the states is substated. In a survey for this we the states is related and the the substates. The survey for the testing test

1-3 is the entry given by the starfiels as it while eminet

the restatates of the spring. As 2 the glass plate and slid

and the state of the state of the second state

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::

though i table:	Strength of pull (2 on fig.)	Releases at (3 on fig.	the re	3/2
	2 g	15 g	3/2	7.5
	(3 in Sige)	(3 115 (ig.)		5
	5 9	27		5.5
	6 18	21	2.08	3.5
	9	24	2.6	2.6
	12 30	36		3
	18 (455	2	
	area 18 18 av 18 2.0	68 The 57 54 av 1	2,00	11 3 10 0
	bold 18 it is to pull.	60}		
	The 27 Corendo in the	value of 6610 figura	10 due	2.5

ifie different 33 between the two starfis 84 It is not in any 2.5

100 40

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 <u>Asterina</u> it seems to

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the starfich was able to realst before releasing (at 3).	
The values for 10 observation on <u>Asterian</u> are as follows:	
Strongth of pull	

	(an file.)	Q} 30		(andr no d
7:5		2.6		
ð		20		
6.0		7S		
8.5		22		Section De
8.6				
		35		A STAR
		184		402
A	V0 40	1sa	and the second	o DI fat.
		100		ar .
2.8				
2.2		88		88

Misrogerding the high values of the first three observations due onservably to the fact that cortain of the tube feet were "refractory", -thet is, had not become coordinated in the stap reflex and were simply attanting, we find that the strangth of attantment of a tube foot is on the everage 2,7 times the attanged of pulling the tube foot if doing at these time (ansunt of residence to the stop). Thet is apple 2.7 times as press to state at residence to the stop). Thet is themalyes; a fact of rest the class to endot they actually are subjecting to any; the tube fact of state the the state of the stop). The themalyes; a fact of rest to a the the state of the stop of 2.7. The value of friction is the shore exacting the the stop the starfish inverted and found to be negliged (shout 3 g).

is constant, logarithmic or of some other meture can be told only after much shatlatical complication of data. In <u>Asterina</u> it scome 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::

S	trength of pull (2 in fig.)	Release at (3 in fig.)	3/2
	th to get loose it	18	2
the feets The	18 18	33	1.8
	24	60	2.5
	30	taking the 60 the comp	2
	36	photising 72 molluse	2

ing ar

Here the avorage quotient is 2.06. The tube foot is 2.06 times as strong to hold as it is to pull. vith its orth spines and sugar

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 Pyconopolia from myself and the side of the aquarium.

be fairly constant within the limits studied. In <u>Frencoults</u> the relationship is over more constant, though it has a wholly different value as seen from the following

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a/s	Raluses st (3 in file.)	Ling to stin
S	10	
8.1	166 M	13
8.8	60	24
\$	1 08	11 80 × 11
R	72 12	36

Hare the average quotiant is 2.06. The tube foot is 2.06 times as attend to hold us it is to yell.

. The difference in the value of the figure is due to abodthe vis of for al fi instruct out and assess some in any why car at for mode with a bility of the tube foot to attanch when not in the Loometor wiste. An attached atationity Autorian is very casily remyed from the substrate and only once have I seen a tube foot torn off in the process. On the other hand Freme podis the staniment to tants much auto fican at xofter gote out gairub feel edus vacai to nous dity blod eless adjuste granoliste and di mede blues . entretak tenactor to the substrate, that it was only with and petiones and the loos of many of the animals twos fort that I could pull it loose. when the starfies was ones walested from the substrate, if the terdenoy to attach continued, us it often did, i was contronted with and unterester to dues increasing eran down has studiitly dilawse and animal from my own names. I have spont the bost part of an hour dismora alleganory ind had a star of an elghteen indh lygonoredia from multisups and in side of the aquarium.

Strength of the step reflex (Pulling ability)

Not only does the ratio of strength of attachment to strength of pull # wary between different species, but also the pulling ability

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 molluse 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.

considered alone. For instance, a small specimen of <u>Pisaster</u> 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

animal dees not wall open the birails proy, as do most of the

other Furcipulate, is the fast Durt under eshor conditions as well, the labe feet, though hisy can tightly attack, do not ordinarily do so then pulling, and consequently the entrations and ordinarily

(tillide antilus) wafter note out to strangt

Not only down the ratio of strangth of stanizant to strangth pull f rary between different species, but glas the pulling ability

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Scholanness (1996) states that a staried (Astarian glassia) is to the drart a pull of 1350 g in opening a bivilye, to which pull the will repre take al suchthese friendlingers rebar, the short order. studeon of radiat boucarth ere deveror, find and matroesen to body e strangth of the standing reflex because he recorded the pull that bloow doline flow and for bus your and acould the pull which would and to eradeleden i the longitudine immediated introduce of the be feet. The mount of pull exerted by a tube foot, under coult tions locomption at least, is as we have song from one-half to one-third the strength of stablight is that moment, Scholagist in this teresting paper also lists five ways in which the starfigh has been possed to open Oysters: (1) by taking the sollars by surprise, (2) besetting the overter so long whit is would be compelled by hunger d want of air to open, (3) by hyperfilled the sollness, (4) by bowing rough their shell. (5) by polynoming them, 511 of which he shows are listicate the shell. (51) by polynoming them, 511 of which he shows are the starfish a body heat, by which it Mills its pres, derived no ubt by posta analegy from the stars of heaven. He himself balleved alous has easier foro off div recens and asgo selly delivers and as . clauson wit is in a some and a

and derived alone. For inserance, a mult appointen of <u>Marmins</u> about one is dismeter was attached one pour to the recording epring and house to pull scaines it. During the whole attarneou the tonaton ried between 40 g and 60 g. The diret was removed and the animal left aging at the thread all night. The next morning it was pulling in the day verted from 55 to 190 g. There are an anna activity of the be feet when the animal was going forward or being pulled walk by the ring. Then the animal was going forward or being pulled walk by the arrested in the animal was going forward or being pulled walk by the streated in the vertices phases of the stationary tube feet wars sould and ring. Then are actended forward at such an angle that they acut arrested in the vertices phases of the step redict so that only a streated in the vertices phases of the step redict so that only a streated in the vertice forward evening the such an angle that they sould action of these area actended forward of and an angle that they sould an arrested in the vertices of the step pulling increased and the section of the animal forward evening the pulling increased and action of the animal forward, forward at such an angle that they sould active between and also pulling the pulling increased and 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 of to be woll over 2000 g. Such a startist 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 tion during the slop-resizer, to how 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 7 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 thear pulling ability.

The case of Pycnopedia # is different as we shall see later. 2545 19.522343

tube feet dauned

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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 <u>Astropecten</u> 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 Pyonopodia is grouped in the Forcipulate with Asterias. and has tube feet, incontradistinction to those of Astropecten. capable of tight attachment, it swallows its foot whole, ejecting d the indigested 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.

225 g. This came from a' sudday increase of pulling as shown by the curve and resulted in the and brasking off where it was tied. The animal had thus pulled steadily at a tension of from 60 to 226 g the a partod of over 35 hours. Another specimen 18 cm in dismetor sulled 300 g when it whe released for fear of breaking . BUG ET AGAA BEST Correlated with the met that Astaring never attaches as estivity as does pinastor is the fact that it never pulls as hard. a 10 en Autorina, registered pulle of 60, 77, 69, and 46 g. in four successive trists. A smaller (Sam) but more active Arteria s tails bedanay ad bines synns all the dasg ad .gee ballad gradual ascent of about 30 minuteer. The decile would last from one to two hours. Soin the dealing in the height of the curve and the fact that the pull did not lost long, comparatively, are permaps, svidendes of fillen. To test the mile of the attaching reflex in this response, the anisal was put on sand and out to pulling in the same way. The (reder at addier). a of A .. A for anot blues at fing and erraduae dish way laid on top of the spingl. This increased its we raining adding to implet to gailde all an all the Adding or which to eldetoetage on show eduction biles a no galiling mode motoente difference in whet willing ability. The dras of Frenchick's is different as we shall ass inter. Scheinstel 1896) states that with respect to thed taking. startish may be divided into two types, there that swallow their the source and the second and the source is and the book the second the secon asing the spilling it to the soft parts of the malles. (Asterias Altered div metucinal in the ground is have a checked with and has tube foot, incontradiction to these of Astronation animal does not pull open the bivevic proy, as do most of the other Foreigulate. 18 the first wat mader other conditions as well,

the tube foot, the date they can then by attach, do not ordinarily do so when pulling, and consequently the antiant can not pull very

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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 lover pulled 54, 45, 30,60 g. in four trials (on different days). The time relations were similar to those of <u>Asterina's pulling reaction</u> (less than half an hour of increasing tension and up to two hours of declining tension).

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The remarkable fact that this large and active starfish should not pullmearly as hard as an 8 cm <u>Asterina</u>, or less than one fourth as hard as a 12 cm <u>Pisaster</u>, 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 directevidence as to the status of the attaching reflex in the locemetor 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 bading "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

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to define a source of a factor of the sale of the sale of the this reapost was about 50 as in diameter, with, socording to Verill's estimate about 23,000 tabe feet, each of which was extremely active. In mater the animal weighed only 50 g, but in air the weight was estimated to be well over 1000 g. Such a starfiel when est to pulling against the recording lover pulled 54, 45, so, co g. in four wrists (on different days). The time relations were similar to those of <u>letering</u>'s pulling recordion (less than helf an new of indreaming banator and up to be two hours of declining tension).

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and the glass. It also involved the wrenching loose of a number of refractory tube feet.

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

could pull about 32 gm.

COORDINATION OF THE TURE FEET

Preliminary description.

When starfish were suspended and the tube feet at the end of one of the rays 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 (Roman's and Ewert 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 ambulacial 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

nervs and will account for the above behavior.

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nd the glass. It also involved the wranshing loose of a number of sfractory tube feet.

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On sand it was found that the animal could pull 16 gm

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Then startish were suspended and the tube fast at the end fore of the rays brought in contact with some solid object, those hat touched it first were usually observed to attach. Then the eighboring tube feet oriented and extended theselves in the same irrestion as the estached tube feet. If opportunity offered these ther tube feet attached to the first tube feet.

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Revenue apaten, the mechanics that it rests in the embalant errous system, the mechanics of this coordination is very observe. Apysiologically, it is a fast attacted as for as I as aware by all of the vorkers on this phase of cohinedons physiology. One tube hot seems to "imitate" in its setivity the behavior of its naighors. In the following analysis of socialmetics in the tube fest and anall inquire into its characteristics in the rigid starfish, and compare it with the coordination manifested by the gills. We shall also inquire into coordination 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.

Coordination in the tube-feet of the rigid Matarfish

When rigid specimens of Pisastèr 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 sourse, so that it may not always reach the farthest tube feet. Later the tube feet word 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 X3uenet (1888), Ludwig and Haman (1899) Meyer (1916) etc., X 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,

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dily 31 erected has . Asiries blair out al soldalestosrado the coordination manifested by the gille. We will also inquire inch acondimication in tube fact of antive but non-oriented starfield. the building up of this quordination into the bailing and the behavior of the striften unter the influence of the unified tobuy oslount bolting cit? to aveb patter of on bas calugat .short thush Instante bas Instant qualyer Courdingtion in the tabe-feat of the rightenterrish When right anothers of Planeter were suspended or inverted the fulle for and a start the tenteraty retrection from the attends. tion of loosening, when found to extend more of loss at fight angulas to the body of the ray. There were subsequent movements of the may which will be considered later. Seme of the tube feet worke them a bismulated to retriet. Shere was a wave of retraction pacaling slang the lines of the two foot. This lanced in intensity as it proceeded from its courte, so that it any not oluque reach the farthest tube foot. Inter the tube fact www arain extend the wave of extension passing back in the reverse order so that the take feet adamated to retract and thats nearest then will . Ensites to taski and a molessing for this coordination is retriction and extension it is not abcomment to hypothesias very complex conditions in the nervous system at the base of the cedicale. Histologically according to XJunnet (1968) Indets and Hamman (1899) Moyor (1916) etc., X. Ste antitation o glaten et di semue metete evertes lavasludme of the marys not they are an ever the outside of the modernal sheath. Bo is as a sure work is a sureholouital evidence of synapses in the correst system of staringing, though of course the evidence on this measion is far from complete. A single, arrest and will a socues for the above being rior.

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 1914) these conditions may spread in any direction (within the ambulacial 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.

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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 an excitation movements in any particular direction in the gills. imulus while will cause the contraction of one group of the (dorsal) gills, will be communicated to others near these and cause XNEXX Summings 1902 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 addirection to opposite direction from 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 ambulactal gills in Pisaster also shows evidences of polaryation similary to the

It has been and that an included twin for will not contract or expend quite contaily. Correct conditions then my be said to exist in the nerve net at the two or the stimulated tabe foot, which affant the mandes of the pedded and angula and gauge the nervel withdrawal (or extendion) of the tube foot. How in a secret with the well known laws of transmission of excitetion in a nerve net (Ferther 1914) these don't them any epond in any direction (within the anounced) and the secret has any statestion or extended of other provided and cause the secretion or extended of the interval and cause the direction (within the anounced) is normal of the tube for the statestion of extended of the tube foot will account for the statestion are anon simple condition will account for the physiclogical estatestion of the tube foot and their account to the location.

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as refinite eving at affin out in inscover to veoloisvin ent that of the tune foot in the rigid starfien. Although there is Istatel count to noiscluding on al exect does al incover fatedal To manut margamente in any partioular direction in the class A-elaubie while will cause the contraction of one group of the (darmal) mills, significant of the state how how how and share and on the states of Illy said their retriction (Jeonings 1907). In this region the norve you noticating of lo berge one that the solution the delive at set be in any direction. The wave of re-extenden manily tales advection Letagizing and it . noligentant to fed and solicerts of leaged restar then antistical. If the mays of restaction is sufficiently Tient sylowni ban cost edus ens es heleniment od yan li saoula retraction as well. The setraction of the build foot does not involve the retraction of the (ambulactel) gills (he most & Chapeaux 1891) an evidence of polarity in the morve mat which succeeds something in the nature of a synapse. That mirt of the narva not which extends up the sides of the long amountaits in the Edit of trailinks solderras or polargation similary to the

polarity of sea anemone tentacle (Pailser 1918) in that when stimulated at the base or middle, the musculature, especially the circular musculature, below (proximal to) the locus of stimulation contracts while that above (distal) does 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 parature 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 watef like a miniature "sausage balloon" with a trunkaged 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.

Ciliary currents in gills.

One of the gills, when thus removed was seen to endose 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.

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Coordination that involves some orientation of the tube feet. Having studied the coordination of the non-locomotor tube if feet and compared that with coordination of the gills we shall

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Parter polarity of sea anemone tentente (Friler 1918) in that when stimulated at the base or middle, ' Une musoulature, especially the offeular musculature, below (preximal to) the locus of stimulation concrected while that above (distal) doe not contract. If stimulated at the tip the whole testadle contracts, the circular musculature responding to a leaser stimulation than the longitudinal. If out off at the base with sciescre, the adges of both the stump and the ablated piece adhere together along the line of the dut by means, seamingly, of a sticky substance on or near the out edges, so that the wound does not open an phinkture to the exterior. The stamps of course sirrivel down in strong contraction. They are found, three days ister a little short but with the and healed over normally. The statest gills show no sign of contraction, and the out and being sealed uver a describedabeve, the gill remains distanded by its enclosed water like a ministire "studge balloon" with you al anticipated and. The contraction of the gill musculistary a aufficient to collapse the gill against the resistance of the closed end. If this and be reased open gently and then the be stimulated collapse enouse immediately,

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Coordination that involves area orientation of the tobe feet. Having studied the coerdination of the non-locometor tube now take up coordination in the behavior of the tube feet during their transition stages between the locomotor and the nonlocomotor 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 attachment already seen, they will attach. This is usually followed by increased activity of the nighboring tube feet and if the starfish is not too rigid, by ther active bending **O** their the toward the stimula fedicareaion. 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 adherging 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 a appear are very inactive or very rigid, and is apt also not to composition bedow 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

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now take up coordination in the behavior of the tube feet during their transition stages between the locameter and the non-

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If a right starfish be suspended and name of the extended tube feet be brough the contact with a solid object, as as have already seen, they will attach. This is usually followed by increased activity of the afgenboring tube feet and if the starfish is not too right, by bow active bending of their tage toward the showing feet and of the star bending of their behavior, that the beginning of the step reflex can be alloited by proper stimulation.

Coordination to measive morenents of tube feet. al schword ed sool edus anol a delivista a cous no li file acid with a small object, such as a penall peint the disc will attadh. If how, the pendil point be moved, with the tube foot still adherding so that the direction in which the tube foot is now pulled out is different from thet in which it originally a extended itself, ether tube feet will Chenceordinate themselves, here lugit a 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 dourse and not to show itself in starfigh that a appear are very inactive or very rigid, and is apt disc not to open yer al estuant besenthroop, beiren vignorie a at erent hi . Lie te verbed some other direction. Out of thirty trials on starfigh in ovides has bedram flew asy crow setate facture lange, another . seeillin in inemeron eviseer of melishibitooo adat and inene those of a star bis bis alter the tabe foot and this contract of flonor the ganetic the bard times in the herd beiere unling the tot foot over in its new direction. I could

observed no difference in the accuracy or promptness of the coordination. I have even untwisted 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.

Coordination of the tube feet in the active starfish.

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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 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.

Tendency of each ray to migrate toward its tip.

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 white 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 anusing to watch this suspended animal industriously

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observed on difference in the escurecy or promptmess of the coordination. I have avon univinced the tube foot spuin, in its new position, without either distarbing the strachment of the tube foot or the coordination of its fellows. Modifed to say these analyulations had to be done with extractors are to avoid stimilations which alght endes retroubles.

Sourdinalized of the fulle fail in the solice starfield. Thus for we have been discussion enoughed coordination the two fort of right non-locomotor subscieve. But then a very large mucher of take fort are seen in the companied sportman, pointing in one direction in destributed infinit, one is upt to be depling with a sear-

If we suspand a starright that is active, het and definitely eriented and isomerchap in any one direction, we find that the tube foot at the time and for a considered or which towers the dish are ortented and antiraly facilate out towing the tip. Proper stimulation of the tube fact at the onde of these rays will slight the step reflex in the direction of the tip of the ray. This would indicate that and ray has a tendency to higher in the direction is would indicate that such ray has a tendency to higher in the direction is would indicate that field is a tendency to higher in the direction is would indicate the such ray has a tendency to higher in the direction is winter.

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Another indication of this tendency is the fact that in stale water or under the influence of chbroform (Mmore 1916) a starfish is extremely sumceptible to autotomy <u>Pisaster</u>

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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 ætion 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 worden indergoing 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 as 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 firs 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 spteads 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.

Another indication of Gale Senderey is the fact that in stale water or under the influence of chiroform (Mnore 1916) a starfielt is extranely surceptible to sutchery, Pissolar

sound much more sumospitite to this remotion if the nervous system has been injured in some part. As I have observed it the resolution consists in an exaggerated tendency in the tips of the several rays to algrate in an exaggerated tendency in the tips of the 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 starfloh. This is one to a pathological alugatheness in the solution of the tube feet in the standishines in the solution of the rays of a pathological hereated and the the interval starfloh. This is one to be the tube feet in the singlemess in the solution of the contral part of the ambulaeral metrous syntem as asset from the indo that the tube feet in the test decider as asset from the foot that the tube feet in the intervolue syntem as asset from the foot that the tube feet in the test decider as a set from the foot that the tube feet in the test decider as a set from the foot that the tube feet in the intervolue syntem is the tube to a pathological and the tube feet as the tube to a presented appreciance of its sentrary, an the attent the set the same of a finality at or meet the band.

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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.

General statement of the mechanism of the positive response.

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 this spreads to the rest of the starfish, involving after a time every tube foot in the body in coordinated locomogition.

General description of the negative response.

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 an exact second in 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, for the those 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

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formation of the "unified lemiles".

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

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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

Phenopodia.

<u>Phonopodia</u> 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

(Fig 11) animal ter sector and the above, with the tube feet at the tip of each may orinated in the direction of the ray, and ready to give the step reflex upon proper stimulation. Now nuch obstantion has convinced me that a positive stimulation at a will found in the increase of coordinated activity in the region of , the gread of this coordinated activity in the way 1912 the last ofter the retraction

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which is in the test from the source of stimulation. It so doing they come is contact with the substrate and execute the stap reflex. From this point on the coordination completes iteelf in the mean memory as outlined for the position tempones. In case the stimulation (is not sufficient to course the returnition or insettivation of all the tube feel, it will obtain a the tube fact, to a certain extent so that the fortheast tube feet and the news solive and berefore will dominate in the

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in very favorable for a study of the magnenies of cordination in positive and sometive responses. The active but not evicated

eminal can be represented as above, with the tube feet at the hig of such may evineted in the direction of the may, and ready to give the ever reflex upon proper stimulation. Now much observation has convinced as that a positive stimulation at a will result is the increase of conditinated solivity in the reader of a the spread of this coordinated solivity in the way

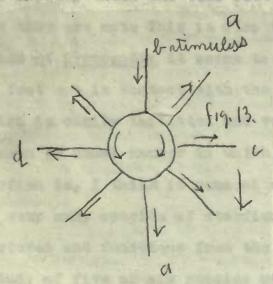
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$(F_{19,12})$ diagramed above, Inthis way $\underline{6}$ and \underline{d} will be coordinated before b though b and the neighboring rays may be more active in their coordination than \underline{c} and \underline{d} because they receive stimulation through the ring from both directions simultaneously.

Now with the negative # response, conditions are different

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 bothet the divergent pulls of the various rays, which as we have seen results in autotomy.

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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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disgramad above. Inthis way frank & will be deerdinated before b though b and the neighboring rays may be more active in their coordination them g and d because they receive stimulation three beer rays from both directions multaneously.

A list adda tive response has been described by loeb (1900) is terms of observations by Norman (1900) as a result of the retraction of hube fort on the inreally stimulated ray and a consequent determination of theories is anarted by the other rasponses by a "parallellogram of forces" emerted by the other mays, each, hype Matidally as I take it, continuing, during the action the work of Bonames, Freyer, Jentings, Eaceda, Oole and others that all normal legamotion is brought about by the cooperstion of all of the take the brought about by the cooperstion of all of the take the provide the and not results in a suborder stepping in one direction and not results in a suborder all one direction and not stion of all of the take of the various is brought about by the cooperas the direction and not are a strong in an and not as the direction of the take of the various is a shick as have the stion of all of the take of the various is a shick as a start of a sea as the direction of the take of the various is a shick as a seand not

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Whether this increase is only relative or to what extent 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 feat, even after (200 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 feat are executing the step guld a regard reflex than where they are not. This is also true of <u>Pisaster</u> 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 cutline. 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 <u>Pyonopodia</u>, <u>Pieaster</u>, <u>Asterina and Evastorias</u> 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 <u>Pyonopodia</u>, the response was analogous to that to contact.

Orientation as a result of stimulating the dermal nerve net or a general stimulation of all the tube feet.

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etuies this increases is only relative or to what extent it is a haclute *VRO 64 PLCARE TRB And ston of the ston reflex in the spreed of goordination. the function of the star reflex in the spread of coordination r probably very isportant. The plaching of one ray of an Asterias will and prompt memories lowencelon with all the tube feet noordinating. sources, the starting is inverted the inverters in it this is the inverters, one testic nove . seet sdal and in all all anthony of and feet. aven after a serveres pinching. The only difference between bis animals is these to positions is that the test of the lost of the involved starfield are not sen of notification territor of all events there to control withulation to net anticities and an interest and enterest and an of origination geade much more register where the table for any amountains the etap where there they are note this is also true of Figgator to a lesser thent, but in case of Frenometa it seems to make but little difference all. .fon to be readed with a social with the second of th . Lemine aids ut ovidos view bas betsidint vilone at saluget betenibro the sources or usual menual is which the second to normal . formed in starfield is. I think in general accord with the above outno... There are very many excesses of starfies, each differing more or and in its atructures and functions from the uthor so that ideas dovolvered and sil tan debin selongs whe to avit to thuse and mort bev. allo of the theusends have to fis ? antrefuers has setucist, retenall, sthougary, sees eval I anolisitatimile feeless bar desines most when so besud insite the Long noth how de boulling mannes out at thes whill be a bound the month these been of direct sumlight the Shrown the eye-woot of Fygnonodia, the west and the second of the sould be the poster of the second se brin Lamb the anti- attaulation in allow a second bring atest supt sit lis to holdslunkin Isronen a na it The responses of the starfish to light # have been divided by Plessner (1913) into two categories those (both positive and negative) in which the eye spot acts as the receptor and those in which the receptors are distributed over the surface and connected with dermal nerve net. Inasmuch as it is the whole surface which possesses these receptors and not merely that at the tip of the ray, it would be well here to look into the qualities of the orientation of the tube feet and their coordination that can be brought about through stimulating the body wall.

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 soon 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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In the above experiment we have an explanation of a <u>positive</u> response to a dermal stimulation. A negative response can be regarded on the above hypothesis as a positive reaction toward the unstimulated side, if it should indeed prove to be a fact as indicated above that a direct response to dermal stimulation is only positive in its sense. Thus we may suppose that the tube feet are oriented toward the side which receives optimal illumination, rather than that they are oriented

The older observers on the responses of starfish to light have divided themselves into two schools. One of these schools regarded the eye spot as a light receptor and in it may be listed Romanes and Ewert (1881), Graber (1885), Preyer (1886), Bohn (1908). The morphologists favored this view also. The second school regarded the light receptors

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

dirachly on the tube feet and those adding on the terminal tube

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

otor starfish,

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

as in the densis or tube foot. Hangold (1903), dowlos (1911s), kast (1911), and sthers admored to this view more or less explicitly. The ingenious experiments of Flosner (1913) have made it seem quite probable that the starfish responds to direct illusination of the densis and that the eys suct receives stimulation from distant areas of light or shadow to which the starfish responds also. This results is a very puzzling aggregate of reactions as the controversy attests.

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The factors which dauge a change is the physiological enterior

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 thy elicit they can therefore be grouped into (1) the positive and (2) the negative. With respect to the receptors on which they deperate they can be grouped into (1) those acting on the dermis and directly on the tube feet and () those acting on the terminal tube feet of the rays (or eye spot which is a modified tube foct). Such common factors in the environment of the starfish act chemical stimulation and text light have been seen to effect the hnified impulse in the uncoordinated starfish in one of 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

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

body he a

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. Theela Retreasers again a Typelves 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

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are essentially the and at hous which determine the anterior as the involve is being forced and operate through the many modernian. Alsh respect to the sumpe of the specifies which the edicit they can therefore he prompt into (1) the positive and (2) the angestre. Mich respect to the receptors on which the departs they can is crouped into (1) these acting on the terminal who directly on the table fort and which is a modified the terminal who had acted the same (or ave and which is a modified the terminal who and the inequies in the uncount which is a modified the the fortier of the acted to be uncounted to be the second on the terminal who and the inequies in the anteritor and the high is a colling on the terminal terminal stimulation and terms the high the second field the the fortier of the above continued anys and it will be seen from the following the area acted in the monortineted inpulse one is is a content of the area of the contributed anys and it will be seen from the following the second acted in the same will be seen from the following the second of the the second of the second from the following the second of the same of the same of the second from the following the second acted in the same will be seen from the following the second acted in the same will

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We are of the may sign of a minimum might sing actively under the influence of the "unified inpulse" bruchwageingt the side of the equarium the time fact is the and of this my have been area protroted out catively. Done behind then coordinated and soon the eigention of locenction complet and the unified was mainting up the side of the equation

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Chemical stimuli # and light (acting on the eye spot) have also been seen to affect the locomotor starfish in a way wholly anal-

Romanes 1883 states that all of the under side of the starfish is sensitive to odor (chemical stimulation) while Prouho (1890) localized these receptors in the terminal tube feet of the rays.

ogous to the above.

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.

of the locameter starfield are not the separate and distinct unities. that they appear above, All of the factors that we have recognized are usually at work at one and the same time. back about as quickly as the tube feat become active again. Onemical stimult & and light (acting on the sys spot) have also been seen to affect the locomotor starfish in a way wholly anal-

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Physical evientation may involve three factors, any one of which may be more or leas beamletely predominent. 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 samping of the anterior rays in the opposite direction: (5) the recordation of the tube field on and side of the starfish and the donsequent samping of the autorior rays in the opposite direction: (5)

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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 (Plessmer 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.

GENERAL CONSIDERATION OF COORDINATION

The categories into which we have analyzed the reactions of the locomotor starfish are not the separate and distinct unities that they appear above. All of the factors that we have recognized are usually at work at one and the same time.

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Direct priestics of the leading ray or rays to one side is dependent upon a unliatoral stimulation of sither the dermis, the eye spot or the tabs foot of these rays and a consequent orientation of these rays toward (or away fram?) the stimulus. If the stimulus acts also on the rays that are situated on the aide of the starfish from which the stimulus comes, the anterior is it the be shifted (Flessmer 1913) to these arms but if it some only on the side of the enterior arms it is nows likely to cause a rotation of the animal as a whole. This is dependent upon bus delivers of the stimulus to the direction of the starfield various other factors that have been analyzed by Bohn (1988). In relative acceleration and retardation of the lateral beditness evode edi lo tipper vressense a servic lo al amus la teral movements of the anterior rays. As a result of etimulation the same factors which we have discussed above actove to aimteb , deet offic ent on the tabe feet, dermis or eve bluow guildenib evilegen a ni bas noti releoon seure bluow dogs cause retardation, provided the Stimulus did not reach the reliance end in anit (neltelumite toerib a of) evidence eron or posterior rays. A mechanical chatals to the progress of the at ende of the sainst will result to oble on a ever - oreging and at opacedo a syleval tot yes an yes that noites out the du gaineard ent and "noiteer noitelyse de the .esiugai betenibroos ent lo vitau lenolionut MOITARIEROOD TO MOITAREDISMOD LAPECHED

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The estegories into which we have analyzed the resetions of the locomotor starfish are not the separate and distinct unities that they appear shows. All of the factors that we have recognized are usually at work at one and the same time. They are nicely balanced against each other and any stimulus which upsets the balance by adding to the strength of one factor or taking from the strength of another factor results in a more or less radical change in the behavior of the animal. It is often difficult, moreover, to discern the cause of a change in behavior, so delicate is the balance between the different factors, and so impossible is it to keep track of the changes of fatigue, hunger, etc., that play an important part in the relative irritability of the animal as a whole, and of its different parts from time to time. An analysis of the behavior of starfishes, based upon observations and experiments on only four or five species, can not pretend to completeness or to a generality covering the whole group of Asteroidea. (See Mangold 1908 on the self burying reaction of <u>Asteroidea</u>).

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 Uexkull, 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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They are mooly balanced sgalast each other and any stimulus which upsets the volume by adding to the strength of one factor or taking from the summeric of another factor results in a more or lass radiand charge in the behavior of the animal. It is often difficult, asterver, to discorn the ocuse of a change in behavior, so delicate is the balance between the different factors, and so impossible is is to head track of the changes of fatigue, bunger, etc., blay play a as leales ory to willestrut evisiter on area testrooml as whole, and of its different parts from this to time. An analysis . trages, bas anoir wrond wood wood about do torverse to torverse and to ments on only four or five syscies, out not pretend to completeness or to a generalish covering the whole group of Astareidas. (See in 1908 on the sair burying resoliton of Astronotical." Theories of the mediant in constant of selvoor It is probably true that all startish locomotion involves odul and groups "calloon) bolling" a traci to seenic all in once al

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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 <u>Pisaster</u>) 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.

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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 set in the set of th

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

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the neghading of extention and the to the protection of atemping. "... It has been shown (Cole 1913) that the coordinated inheronor of detries and wette neve not sine the starfield to removed on water and hald inverted for two minutes. This procedure causes lo gaigoord and has (notecall al) feet and the drouping of to arms abortally. When put back in the dish of gas water, the timel usually walks in mearly the same direction as before. THE state and the state the fact the fact the fact the bube fact are guite - series is an indicated this this estenibni . geor does redie betweet on and extension, of which as we have seen, the step reflex is a diffication, is, perhaps, in no way depadent upon or implicated a the mechanism of oriestation. The only point of contact of these to mochanisms is the fact this that both act upon the full fort. a the locost tor state then every tube foot is eriested, whather is seek offer not not anthrests and artending to besterset a re accountioned usually as parts of the step rafler. OTH SUCCESSION OF THE CARACTER DEPARTED INCIDENT OF

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In case of some tipes (femings 1907) of the righting of tenting 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.



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Thus in the above diagram, fig. 14 which illustrates a frequently observed type of righting reaction the rays labeled <u>a</u> <u>b</u> have doubled under and are migrating in the direction of the arrow. The rays labeled <u>c</u> <u>c</u> 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 <u>a</u> <u>b</u> and completeing the somersault. As soon as the righting is complete the rays <u>c</u> <u>c</u> ag

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ing 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

of (Echinoderm) organs described as nervous in function that I have decided to remain in this regard in a state of philosophical doubt."

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Thus in the above disgram, fig. 14 which illustrates a frequently observed type of righting resolion the rays labeled 2 h have doubled under and are migrating in the direction of the arrow. In orays labeled 2 g under the influence of the case unified impulse have turned in the same direction but migrate, after having turned, in the opposite direction, thus aroasing over the arms 2 h and complete the rays 1 g again reverse and migrate in the same direction as the righting is domplete the rays 2 h.

Then, (fig. 18), the starfish was in position 1 it was moving in the direction of the arrow and all of the tube fast were oriented in this direction. However, when coming up spainet the obstacle (3) the tube fast of each my immediately changed their erientation to the direction indicated by the arrows at the tips of the respective rays. This results in the animal neatly avoiding the obstacle and migrating off in the direction indicated by the upper arrow. This is a very interesting reaction and has been made the subject of careful study below in an effort to discover the factors concerned in this breaking up of the coordinated impulse.

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.

ment of the starfield over the unbetrate. (Sac Cole 1913h

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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Spix, (1809) described a nervous system for the starfish that would satisfy such an assumption. Unfortunately, however, it proved to be the system of gastric and hepatic mesenteris filaments.

Accoding to Baudelot (1872) who gives an historical resume of the earlier morphological literature the subject became so controversal that A. H. Quatrefages (1842) made the statement freely translated as follows. "Naturalists of great merit have come to such diverse conclusions as to the significance of the various systems of (Echinoderm) organs described as nervous in function that I have decided to remain in this regard in a state of philosophical doubt."

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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 1913).

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 this direction.

Similarly the righting starfish has set in action by the activity of the rays \underline{a} and \underline{b} (fig. 14) a somersaulting motion on a horizontal axis. This results in pulling the rays, \underline{c} and \underline{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 \underline{c} and \underline{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 involbed 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 metgabore, 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 reasonae to stimuli which affect them or spread to them from meighboring tube feet.

Foneshile physiological explanation in the traction on the tube fact resulting from the movement of the rays over the substrate. It seems to me that the only constant factor that could secount for the behavior observed, is the traction of the substrate on the tube feet. Winis traction is the mechanical result of the move-

The unspold's starfiel (fig. (*) is moving in the direction of the arnow. The various tube feet ney receive stimuli from the substate which result in their orienting this direction.

Similarly the righting starilah has set in action by the activity of the rays g and b (fig. 14) a someraculting motion on a horizontal exis. This results in public the rays, g and g in the direction of the arms that indicates their motion. It is this traction that may oright the two feet. In this connection it is to be noted that if the rays g and g do not troop down to the substrate but the case) their scordinated inpulse does not reverse but remains, as indicated by the parallel extension of the tube feet, is have feet indicated by the parallel extension of the tube feet, is have substrate but the case) their scordinated impulse does not reverse but remains, as indicated by the parallel extension of the tube feet, is hencey with that of the rest of the armallel extension of the tube feet, is hencey with

In the case of the deviating starfish, the axis of the rotetion 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 cases tion of locomotion on the part of the rays on one side of the body, but its continuation (or quick resumption after temporary cases tion) on the other, perhaps the stronger, side. As this continues, due to the comparative rigidity of the animal, there is a pull (f^{egl5}) in the direction of the grows (at the tips of the rays) to which pull the tube feet seem to coordinate themselves.

Direct pull, exerted through the substrate by the movement of the mnimal 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 eridence in conslucive.

The obvious way of testing this is to slowlypull the animals over the stubstrate (see Cole 1913b) and ascertain whether a tendency to locomotion in this direction could be built up. About forty treats 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 fellowed, however, less than half the trials, the animal more often settling down obstinately how hich

When the locomotion did fillow, it was, unfortunately, in every case but one in the <u>opposite</u> 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 it he 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 animale, then for the most part may be considered a result of this stimulation rather than a result of the pull.

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on the other, perhaps the stronger, aids. As this continues, due to the comparative rigidity of the minul, there is a pull in the direction of the arows (at the tige of the rays) to sold pull the tube feet seem to coordinate the unserves. Direct pull, sumrted through the substrate by the movement of the summal and acting on the tube feet, congunating that is originate them, account for the above described beingtor. We shall may tup to the automation for and against the contention that the pull of the substrate does erient the tube feet.

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"Then the locomotion did filles is see, unfortunately, in every maps but one in the <u>provise</u> dimension to the pull. It soutinued for a few on, only, then the second estile down into the rigid state. The one animal that erawled is the direction, "I was pulled, continued to orasi all day. "These results wars complicated by the effects of southest standardian of the dormal surfaces which induces alone standard and assaulten of the dormal antices of the entant. for the most part may be considered a result of this then in rather than a result of the pulle. 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.

I f 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 <u>Pycnopodia</u>. At first the tube feet on the injured ann 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 Bet stuck less and less

fimised my wilked such about in the suctor between the adjacent

stationary raye. I then predded the starfield and three it into a

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I have in fact been unable to manipulate the starfish eq a to exart a stardy pull in any one direction for any length of time dithout exusing the tube fact to attich and hold on, a tendency which has spread to other tube feet and inhibited any coordinated impulse that might have resulted. Estar, moreover, on certain ecoseiens they are been observed to retract and be antirely inactive.

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When this experiment was repeated on <u>Pisaster</u>, the animal remained stationary for five minutes, the neurotomized ray, affixing itself rather firmly to the substrate. A¹ 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 locometion.

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

When the neurotômized starfish had some to rest it was observed that the four intact rays were stationary while the neuroto moized ray walked mank about in the sector between the adjacent stationary rays. I Then prodded the starfish and threw it into a

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stigntly, whill wray bohaved very ware (ills they do in ordinary wet reter incorive lessmation. The arm baing very fiexible, sportinetion did mat scour when we neurotonized afor wes antorner, because it bent around and under before the stude feet let lesse. Some three or four hours after the openation we take the the neuromotized are very all retreated and the arm prestically motionizes. A week later the sound second to have healed and the arm to have regained its at would second to have healed and the arm to have regained its at a take in organized and the arm to have regained its

When this experiment we reported on <u>Mension</u>, the animal remained stationary for fire minutes, the neurotomized ray, affining itself rather firmly to the substrate. A' the and of this time the other rays were seen pulling in the direction of this time the other rays were seen pulling in the direction of their former anterior, any from the genrotomized ray. Some refractory take feet ware seen attaching to the substrates, which is the disc bold of ty the activaty of the uninjured arms. One were arended of by the activaty of the uninjured arms. One refractory. Is an animus coordination was complete, thends and rary solirs. The ane minute coordination was complete, the the refractory the animal valued containation are complete, the two and as antradied and rigid. It was always bound to the neurotomized bound is isometion.

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When the neurocomized starfish had done to rest it was observed that the four intest rays wore stationary while the neuroto motood ray walked mank allow in the apoter between the sheeth stationary mayari then predded the starfish and throw it into a

very intensly appressed state. The neurotomized ray continued as before actively moving in its own sector. The gills were retracted and the pedicellariae open, over the whole starfish while in the region of the cut and beyond the gills were out normally and the pedicellanae at rest. On prodding the neurotomized arm the gills drew in, the pedicellance stood out and opened and the tube feet held fast. This last reaction passed off and the neurotomized arm started locomotion again in its sector. The gills and pedicellaria remained in the irritated state so that the cut did not demark two different areas of gills and and pedicellaria as it had before as it did now with the tube feet.

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 seperted on a number of animals, with very similar results. Asterina responds in this way but rather less completely than Pisaster. Rus 16 P.65

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An active starfish with a e anterior (see pr 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. Be 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.

Ins summials of these unceriments were Hovented

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very intensity supressed state. Thenewrotunized may nontinued as bedoes activaly moving in its own sector. The gills ware retreated and the pedicallariae open, ever the shale starfies while in the region of the out and beyond the gills word out mornally and the pedicallariae at rest. On prodding the neurotomized and the tube fact held fast. This last recoler massed off the gills and pedicallariae testind in the state of that the out did not described in the irritated at a blat the out did not describe in the to be irritated at a blat the state of the before is and in the irritated at a blat the set out did not describe the different areas of gills and and the two out did not describe the different to be irritated at a blat the substance is hed before areas and a state de and

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was pioked up quicky and the rays <u>b o d</u> neuroscentred. The miles? was set as the elds of the equation with the intect rays (a.g) directed downwards, lectemotion followed <u>a.g</u> down the alds and across the aquarter. <u>M.A.d</u> presented refractory take fort and lecters when the animal had progressed shout 6 an soundination was fairly well established but not very control 6 an soundination was take feet were pulsed lecter they retracted and the not recet at all, for sometime. Maighboring take feet, however, should diminished tendency to attach they fort, however, should all, is removing to attach they are first but letter and age to diminished tendency to attach they have been and were and a diminished tendency to attach they and wore and a to attack tendency to attach they are first but letter and and the first were provided by a state that here and a sound diminished tendency to attach they and wore and a sound attack tendency to attach they are first but letter and and the sound the tend to attach the tende, however, should diminished tendency to attach they are state to a state to a to be the tendency to attach they are the totak to a the tendency to attach the tendency to the section of the diminished tendency to attach the first but letter and to and the tendency to attach the section the tendency at the tendency to a tendency to attach the tendency to the tendency to a tendency to attach the tendency to the tendency to a tendency to attach the tendency to the tendency to a tendency to attach the tendency to the tendency tendency to a tendency to attach tendency tend

(near the base)

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I next neurotomized 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 leading specimen. Locomotion down the side was more active, the leveling (former anterior) arms taking up the locomotion quickly and by pulling, in harmony with the force of gravity, forced acertain 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 locomo tor impulse was so well established that crawling continued IP across the floor of the aquarium and up the other side. 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 styppage 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 aaadestate for some time. The rays that became active first were not contiguous, $\frac{1}{\lambda}$ and e, while b d and e remained attached. A and e moved about in their sectors at random all the afternoon. The next morning the starfish was in a moribound condition but had migrated across the aquarium during the night.

The essentials of these experiments were repeated many

I north nourotomized ands and of a rather large starfieb that was not very notive. I "started" it on the olds of the aquarium with its former "enterior" desemand. Issamotion continued down the side until the dise was should at the angle of the wall with the floor of the aquarium. At this point, the animal secured the wight state and would creek no farther.

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The startish was then taken up and stimulated hership on the various mays. The sainal assumed the rigic state when wet down the tube fact hains their standard, and remained in this state for some time. The rays that became softwe first were not conditiones, a smooth to the rays that became softwe first were not moved a subt in their sectors at random all the afterness. A and o next working the startich was in a maribound condition but had algreited stress the equation doring the dish. 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.#

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 conducted movements of the tentacles in <u>Synapta</u> and coordinated movements of the body muscles are not destroyed by cutting the nerve ring. See also Grave 1400 on <u>Ophuira brevispina</u>

Among those who report the opposite results are Vulpian (1862) Krukeuberg (1881) DeMoor and Chapeaux 1891 Loeb (1900)-Mangold (14040 14044) (Moore (19109, 1910b) e 12

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 1914) transmission pasta cut in the ambulacral nervous system, there may be a certain limited amount of coordination between parts separated by such a cut brought about merverstet through there 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 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 as state, 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 anim al was in a state times with reaches thetraried between the two arampics dited. It was found that if the manipulation was rough or unnecessarily prolonged, the animals rould become rigidly attached and would not he constants for same time or at all while some apimals refused to goordinate with own the gentlest menipulation.

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of active locomotion, the rays that were anterior will crawl on into the tubes while the rays that were posterior will start to crawl out of them. Usually before one of these rays leaves go its hold on the float, or at any rate soon afterward, the impulse in this ray is reversed and it is seen to be active in its migration toward its own tip, regardless of the direction in which the other rays are erawling. If now the tubes are removed from their floats and set on the bottom of the aquarium, with the tip of a ray in each, the coordinated impulse is quickly re-established and the animal migrates back ad forth within the confines set up by the ends of the tubes. After extensive experimentation with the reactions of Pisaster in these floats, I have very seldom seen the unified impulse appear when the floats were free to move separately, and having appeared it seldom lasts more than a minute or two. It appears quite promptly and lasts for a long time (an hour or more) if the tubes are not separately moveable but are resting on the bottom of the aquarium. Pantana in 215.07

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 hand 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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of active locomotion. the rays that were enterior will creek an into the tubes while the rays that were posterior will start to arguit out of these. Usually horors and of these rays loaves an its hald on the flest, or at any mate soon afternard, bu of most in this ray is reversed and it is seen to be adi to enclorence , dis ave the own the own the reardions of the direction in which the other rays are drawling. If now the tubes are recoved from their fleets and set on the bothes of the aquistion, with the site of a ray in each, the section ted impulse ting he food seterate feater and the bas base her attains within the confices set up by the ends of the tubes. After at modenaty is encoded at it dis reactions of Planeton in these floats, I have very saldes seen the unified impulse appear when the floate were free to move asparately, and having appeared it notices than a mente of sea. It appeares quite promptly and laste for a long time (an hour or more) out no malicer ere tud eldeeven vieterages fon ere cedui eni 11 .multaupa bris To mostad Supplementary experiments ware earried on with figh free awinding substrates. One, two of three of the rays sere put on the substrate and the ethere alleved to hand over the side on the floor of the aquartim half a on. below. The party on ade aubstrate was aften seen to signate while that on the other of news vilacementing for over and they were not infrequently sher to

algrote in different directions. Of course this would not be likely to hoppen if the substitutes were not separately moreable. From the above experiments it would neem that a factor in

the unity of the coordinated impulse is the unity of the substrate or rather of the saimals relation to the substrate. # 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).)

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.

Deviation reaction not interfered with by cutting nervous connections with interradial area.

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.

Deviation reaction not elicited by prodding interradial area. 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

by means of its suines only. In deviating around an absteals

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

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.

It was thought that the amount of push which the deviating animal exerted upon the obstacle whenconsidered 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 revelving drum. The appearance of the curve was as below for the different species studied.

ted to such other bay are restand as follows. Fulling 15 gr. sull-

Tat and haves

on sand of T.bg.

Readed with 60 years 32 date warder their 23 ges. deviation thereod 55

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 **EXERCIT** 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

Strongylocentroters franciscanus was found to be maving on sand by means of its spines only. In deviating around an obstacle

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complicated coordination of maxamate that are involved in the

Note that he has a second to all the "deviation much" on different and the transmission with different velocities on the animal vary with meathering of and with different velocities on the animal vary with attend and the deviation while quantificative empects of annials it was then it is a bolight the the anomal of push which the deviating with its pulling about the obstacle whenhousidered in connection with its pulling about the obstacle whenhousidered in connection of push was measured by attended the obstacles, a lover, evincing and he above described. The push, then was vectored in connection before of the curve, withink the day of the obstacles, a lover, evincing and he different and the curve, without the day we have the transmission appreciation of the automation of the deviation the recording and of the curve, withing we have the start the recording and of the curve, without on the slowly revolving trans. The appreciation of the curve was as below for the different species attaled.

The point continues to increase until the deviction begins, that is, until the effectors (tabe feet or spines) on one side of the body begin to reverse themelves and the rotation stouch the obstacle as an axis is initiated. From the notation stouch the inregular decline in the peak until the manak enimal is free of the shutacle. With the truncing at the man speed, the daspe of the course as well as its height is dependent upon the set as to get results as founded, This was taken into as a wohn as as to get results as founded, and the set be next and the standard results as founded, the best best and and the spines only. In deviating states the set and the spines on the spines only. In deviating stand an obstacle it takes the same course as a starfish. This case is cited since the spines of the sea urchin do not attach and their behavior in this connection indicates a rather striking similarity between the physiology of the spine and that of the tube foot.

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 <u>Pycnopodia</u>. 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, pullloaded with 80 gm. 32 gm, deviation 29 gm, deviation loaded 35 gm.

Due to the fact that <u>Pisaster</u> and <u>Asterina</u> are able to pull very much harder in proportion to their size than are the sea urchin or <u>Pyenopodia</u> 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 <u>Pisaster</u> (about 15 cm in diameter) is 20 g. on a solid substrate and 6 g on sand. <u>Asterina</u> (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.

about fiab g in each dange This shows

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takes the same course as a starfigh. This case is dited since the ines of the sea wrohin do not attach and their behavior in this conction indicates a rather striking similarity between the physicledy the same and that of the tube foot.

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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 <u>Asterina</u> 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 (<u>Asterina</u>) 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

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nd on send veighted (40c) of 15 g (Res p. 21). The above study f the mechanics of the deviation foes not protect to be statistially comprehensive. The object is mensive to point out that the deviation push⁶ can be always increased by veighting down the animal nd that in the see prohin, which uses its spines, and in Fydnopodia hich does not attach tightly while pulling hard (Res p. 22) the pull an also be increased by veighting down the animal. The relationhigh of pull, and deviation push in the loaded and unloaded <u>Asterina</u> attively to the pulling ability of the animals, both loaded and un-

Thus, the attaching reflex that strangthens with the realsance to the ordinary step [see p. 12] does not appear comparably a the deviation reaction. This it seems to no is because the tube cettor one side of the obstacle overbelance in their traction these in the other side, sause a rotation of the animal in their traction of the various tube feet coordinate in the direction of this rotaion. There is then no resistance to the abeg but merely a deviation. It is one direction or the other brought scout by its relation of the substrate.

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In order that the obstacle may be left behind in the deviation reaction there is usually a turn of alleast 70° 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 criented 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

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a might be expected from the configuration of the nervous system, that he mechanism of the deviation reaction is altogether different from he mechanism involved in a change of direction when the tips of the sys are stimulated. In the one case we are dealing with the relatively constant threshold of the receptors in the end of the ray while in the ther case we are dealing with factors that vary with the mechanical sta of load and friction.

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In order thet the obstacle may be left bahind in the devicton reaction there is unually a turn of alleast 70° which is often acovered from, by the operation of a tendency, whose machanism I have of worked out, to continue arcwling in the same direction as before he distyrbance, even if the action involve an actual change of directon, back, from one assumed as the result of the disturbance. This andency will also be noticed in connection with the righting reaction b. 75).

COORDINATION OF MOVEMENTS OF THE TURE FAST WITH TROSE OF

of the object, an activation of their coordination toward the tip of the may. This will be followed, almost immediately by a dorso-flexion of the tip of the ray. The ray can be said oriented to set ifself more nearly at right angles to the extended active tube feet. This reaction has been observed time and again in Pisaster oraceuw, Asterina, Pyonopodia, Leptasterias, Pister brevigpinus and Evasterian. 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.

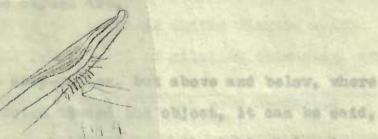
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If, for the gentle contact we substitute a harsh tapping of the tip of the ray, the tube feet will retract and the ray become more rigid and shorter, but without any sign of the dorsal the object in a sort of hollows flexion. ddiw domino.



ly oriented tube feet, this time involving both dorsal and ventral

In the region where the tube feet are undergoing the step-

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T 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 fect 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

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of the object, on active time of their coordination toward the tip of the my. This will be followed, almost immediately by a dores-flowing of the tip of the ray. The ray can be said to eqt if soif and a nearly at right angles is the colored active much take feet. This resolion has been observed time and again in plansing and frantering. Francedia, landestaring, fister brories the mines it is a preduct of local reflexes in Set it is not dependent upon connection with the oral nerve ring, but dependent upon connection with the oral nerve ring, but cours could the sound the time of a nerve ring, but cours could will be active tends of a nerve ring, but

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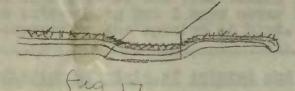
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T ve have seem that if a tube foot in the middle of a ray be allowed to attach to an object and the object he then pulled to one alde. The tube foot with it, ether tobe foot will also move to the same alde and securingly reach out for the object to which the tube foot is attrabed. Now if a sufficient mundt of tube foot is attrabed. Now if a sufficient ray can be said to set itself more nearly at right angles to the oriented active tube feet by lateral as well as by dorsal movement.



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

When The slender armed species of starfish (Evastinias iroschelii) 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,

famm". This is similar to the state of yastro Flooten which

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 stepreflex, there is no bending of the ray.#

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It has been shown by both Jennings (1907) and Mangold (19084)

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These movements is not shown by the instated may from both

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(See also Jonaings (1907) description of the taking of food from the pedicellarize by the tube feet).

We have the element around rounder of starfind (Erectinize broacheld) was suspended and a flat place of the rays. The tube feet, by a thread to the reatural side of one of the rays. The tube feet, estended rather insetivaly toraid the tip of the ray insedictely aters 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 bath shore and below it and the base of the ray so as to receive the object is a sort of follow. The tube feet as student of tube feet bath shore and below it and the bencing of the ray so as to receive the object is a sort of follow. The tube feet

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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 even, 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 (1661) and Neart (1881) who describe this response aptly call " a tulip like form". This is similar to the state of ventro flexion which Houre (1920a) # describes as a result of nicotine pointening, and

The effect of nicotine on starfish had been described previously by Preyer (1886) and Greenwood (1890) which I have confirmed for <u>Pisaster</u>, the chief difference seems to be that the tube feet in the nicotinized <u>Pisaster</u> 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 show.

These movements are shown by the isolated ray from both the nicetinized (Moore) and the rigid animal. Chat as the tube feet earry a small place 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 shove. The behavior of the tube feet when the animal moves its and in under the disc as a part of the feed 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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Montrol Review of right, of inivers and minutifiers abortial. If a Pisaactor in a state of entreme rigidity be inverted there will be as we have geen, a rather inactive extender of the two fact more or less at right angles to the rays. Enere will be an exismistion of the tabe feet at the tip in the direction of the ray. The rays, seen after inverting still life these live state may continue, in absence of disturbing stimulation for as atale may continue, in absence of disturbing stimulation for as and as the base, this state flation have be used to be very and atale may continue, in absence of disturbing stimulation for as as the act the base, the stops of disturbing stimulation for as atale may continue, in absence of disturbing stimulation for as and a solute the stops of the rays company of gain interaction at the stops of the tays company (8001) and form?, This is similar to the stops of the tays contro floring wing form?, This is similar to the state of ventre floring ratios wing Horro (1900) d describes as a result of alcoting point of action store (1900) d describes as a result of alcoting point of action atom (1900) d describes as a result of alcoting point of action (1900) d describes as a result of alcoting point of action wing Horro (1900) d describes as a result of alcoting point of action wing Horro (1900) d describes as a result of alcoting point of action wing Horro (1900) d describes as a result of alcoting point of action wing Horro (1900) d describes as a result of alcoting point of action wing Horro (1900) d describes as a result of alcoting point of action wing Horro (1900) d describes as a result of alcoting point of action wing Horro (1900) d describes as a result of alcoting point of action wing Horro (1900) d describes as a result of alcoting point of action wing Horro (1900) d describes as a result of alcoting point of action wing Horro (1900) d describes as a result of alcoting point of action wing Horro (1900) d describes as a result of alcoting point of a

Fine affect of blooting on starfich had been described previously by Prever (1886) and Groenceed (1890) will ch I have confirmed for <u>Eleminics</u>. The chief difference seems to be that the tube feet in the alcotinized <u>Planator</u> are completely retracted, while those of the rigid, ar of the neurotomized animal show a cortain amount of extension but no particular orientation. The extension of the space is groater in the alcostailed animal glaw.

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

If an active <u>Pisaster</u> 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 micotinized animal in that contact stimulations at once set up activities of the tube fest 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 dies 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 <u>Pisaster</u> suspended and in a state of

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Desertration of various other correlated novements of the

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If an antire <u>Handar</u> to anguaded in wher and awy from control stimulation, the reye nere about for a while, flating theme saives derestly and interally, in a manner that we shall discum later, but eventually assume a state of ventro-flation similar to that assumed by the rigid animal. The active enimal in ventro flat ion differt, however, from the rigid or the significated animal in that contact stimulations at once set as a state the significated animal in and arms. The tabe fact react positively to centils contact stimulation and reprotees of the arms to these stimulations, but the positive and asset we activities of the tabe for the set of have followed the imthe rest of the same to these stimulations, but the positive the rest of the same to these stimulations, but the positive the rest of the same of the tabe for the set of a set of the rest of the same of the tabe for the set of the set of the rest of the same of the same to these stimulations, but the positive the rest of the same of the tabe for the set of the tabe for of the rest of the stimulation be out to here here the tabe for a stratest over the works animal and the arms themesive will become another the strates of the stimulation be out the the tabe for a sit and the tabe for the stimulation be out the the tabe for a sit and the tabe tabe for and and the arms themesive will become

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Description of Mis forsetion of the coordinated impulse when the jube feet are free of the substrates

A strong positive response, on the other hand, does spread, and in spreading involves movements of the srm, as the following experiment will show. An softys <u>Pinsater</u> suspended and in a state of

binum is side of the aquarium so an chethe wall. The tube feet at trotched out toward the wall, 1916 tabfish still farther over 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 oriented the actively extended tube feet which had become coordinatedly pointing toward the wall.

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As the rays a 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 directhey tion of a e 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 dove 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

vontio-flanden was brought oner the side of the aquestus so that the tips of the roys a stouch the well. The tube feet at .Ifeer and browed and baladoria wieviana over amain to agit and and a the dilles began to pull the statistic still for the bear through the well. She tips of the isre a a flaxed dereally and began migra ting in their own direction. In the mention the Lie obviout at as to have the had leaf had soit of the unit anithteod betalog Ils maps stor Holds , Lamina al tort offit bebaring all directly toward the wall of the southing. As the fabric for became extented in this direction, there was a coordinated were died bas fiel oil of bestive i yes .over eds to faceover of news decad bee timit and to bedated to the west base over to the wall and ray g beat directly over the disc toward the wall. Made ray was seen to get thealt more way you chell . Liew the actively entended had feet which had became deerding telly pointing toward the well, As the may als continued boundary, the disc was brought classes to the well and with it. the other ormes. As they souched the wall, sized the bube feet ward eriented in the diredtion of a bound executing the step reflex in this direction and the enlagt started partnetly coordinated and mercal lecteriles (suo need neived in the suspending thread invite deed over all successfor at these areas areas with the right of restation reaction. eds to hold settilized a vierter of fusalizing of the

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widebing resolion of the undeerdimited active <u>Firster</u>. If ve assume that two adjected rays initizes the resolion by attending to the enbetrate with their ventral sides thread toward each other, the shows description will fit the righting resolion with the change of only a few words. The case dereal fiction of the datteting rays and their signation beward their tips will 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 ever 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 Right reaction.

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Jennings (1907 pp. 125gg 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 <u>spread</u> 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 <u>toward</u> each other in a majority of cases in connection with our discussion of the righting of the oriented starfish. he observed. The basis feet will all possible pointing in the direction of the faitisting reps and the other rays will neve as as to done norm of right angles to the direction of the table feet. The atm on the right angles to the the right, we norm over in the direction of the initiating rays. The are on the left will telet to the initiating rays. The are and directly equesive the initiating area will bene directly over the directly equesive the initiating area will bene directly and the left will telet to the initiating area will bene directly are directly equesive the initiating area will bene directly and the left will telet to the initiating area will bene directly are the directly equesive the summany of the the other and are directly equesive the direct of the starting area directly of the direct area and the the attent of the initiating area. This are we shall are is portage the and area initiating rays. This are we shall are is portage the attent initiating area. This are we shall are is portage the attent and the initiating at the direct attent of the starting. Analysis of all benefits the attent of the starting area about which the direct of the starting area been about which the direct of the starting area been about which the direct of the starting area been about which the tray area of a the initiation attent are be grouped. The first type information are

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-64-

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 it which passes lengthwise through one of the attached rays. This method of turning is extremely difficult and awkward but is seen at time." 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 thrid 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 ryAs, 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 till the normal position is reached. (A model of the starfish in paper or oloth 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

Jennings second typede as follows. 2. "The tips of the two stincent rays an trict that the ventral survives de not face each clost, but toth face in the same direction. The tube fact then this mald and throw the starfish ever, twisting it about an axis is which passes lingth. wise through one of the attached rays. This method of turning is extranely difficult and emimare but is seen at time. Venally however """ a third ray (also hold and and alde in the third of "", ixon novin deni to rolitenati a unimust next belien and bus , sould well a wine galingin le berken whil bevread a vad I variations of it (Type 5 (5) of Jonnings) where only one ray attiches a few times also. In sach case the coordinated impulse bas ages to con molificial int and from the fallent ag or mays and involve coordination of the rest of the flow the last and to seen sugar the arms in the manner described above. The say that alght be expected to attach noundine taly (facing) the ray that bands down is usually seen lifted above the substrate and recohing out in the direction of the righting. Locomotion after vighting is usually toward the rays that this is the resulton. Jenning's thread is as follows.

3." Three adjacent rays attach and remain attached, all pulling throughout the resolies. Venally the anight turns primarily by the and of the two super ryps, while the middle has the relatively passive and compatible to decide best under as the submit turns. Offer this middle ray wills beckmark beneath and of these state, or the other sains setively over the embrack opticies is a combination of these the movements thitte mersal popticies is reached the needed of the state is a sufficient to these of the reached of the state and states and states of the reached of the states of the states and the state is a combination of the states of the states which is paper at these of the rays remain states and an attack of such sources and three of the rays remain states and an states of the set set set and there is no new principal involved here, excess that of the passive movement of the middle x ray which will be discussed in connection with the fourthe 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.

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(!)

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. 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 to the relaxed state of the starfish ar 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 anns" (rays & in fig."). Now the factor, which causes the moving forward of the back rays when the direction of the coordinated impulse, as seen by the activety 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 parety arreaded of the stories is ray which will be dischared in connection with the fourthe type. The impulse spreads to the tube feet of the imputation of their relains up ever the deordination of these is followed by their relains up ever the disc and seving the same in followed by their relains up ever the scording to the same principles as described appre. (types 1 and 2).

the fourth type is as fullows.

A. "Tour of the reys take hold, two extending to the right, two to the loft. Inen the fifth ray, (which we may call the neve vilocrib sprive has an inglate bettil at (one tolrescor till die ventral surface readies the bottom, while the antorior body site tolkeshoo out dispuss brandood alisy ting body tra pair the latter willing forward over the surface of the (former)" Inte type of righting is sketched on ---- In case of Plaaster it is nove and to soon if the onlar is the research to relaxed. The sequence of the events as I have observed it is as fellows. The anterior rays twick bowerd such a ther and the delitate dat (at theath of to) teve estates a lugat betallion as in trend trend called and an estimat the .. fort at an la perel rays and the bending up of the posterior may. One to the relaxed state of the starfies when other physiological . sates level their which the the lateral wine assuming fairs there is or ventro flexion, these drane to the dishetrate and become the "protection attached anas" (fage & in fight. Now We factor which causes the newing forward of the back rays than the direction of the coordinated impulse, as sean by the solivity of the ai national sites of an in the strength and an the spectra direction is the same factor. I think which causes the complem coordination of the deviation readtion. I have presented the evidence which titu ab at sei actieve at resert of fails to ac abeat

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.

to allian. I have

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 the tube feet become oriented in the direction of the pull and righting proceeds according to method three or four with possibly a (release)lifting of the locomotor ray free of the substrate.

Jenninge 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

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the relation of the moving parts of the animal to the substrate and a consequent erlantetion of the tube feet in the direction of the mavement.

Jennings 11572 type is as follows:

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

The method of melacon as 1 have observed it is of two Mands. (1) he pull of the other parts of the starfleh tear loose, attach but mmelly not so therizily as those that were first attach but mmelly not so therily as those that were first stached. As this continues the tube feet in the region in question sither all become retracted and the my is pulled free of the substrate and sume over in the righting, 40 he tube isso become arished in the direction of the pull and righting proceeds succreding to method three of the substrate. Sitting of the looms for rey free of the substrate.

with his second type.

Journa's seventh type is to follows:

*(8) 7. A still more unusual type is seen in the performance of the righting solian althout attacheset of the babe feet of any of the rays. Freyer (1880) and Hemmes (1882) here given account of certain anys in which this is schethnes accomplianed. The typical method seems for the schethnes to raise its disk bigh standing on the tipe of all in five rays, these its disk one or mare rays over, or and ar more under or both until the body Sopples ever ventral side down. In my own abservations, these wave experimentally provonted from table hold. The startish the wave and and any own abservations. The startish the wave and and any own abservations. bizarre forms, until it had succeeded in getting its ventral side down, when, the squirming ceased."

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The method of righting, described by Romanes and Preyer ect seems to be confined to Astropicien 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 of sand.

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

The behavior of a large sluggish Pisaster, when inverted on sand is interesting in connection with Moors (1916, 1918, 1920g 19204) 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 patts of the rays. For some time all five rays remained dorwoflexed. When the animals win placed on its ventral side on the sand, there was still avery 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.

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These results are probably merely analygous 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 **pre** representatives of the asteroidea. I have, more Cover, so far been unable to get in <u>Pisaster</u> the marked dorso-flexion which Moore figures for <u>Asterias forbesi</u>. bizarre forme, until it had succeeded in gatting its ventral side down, when the squirming despect. The setund of righting, described by Romanes and Freyer

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Description of the righting reaction is sconre rised the tube fast are prevented abtequing by inverting the appeal of man. With the animals at my disposal it was thenght peesible to

provent the attaduent of the tube feetby investing upon and.

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These results are probably merely analygous to these of Moore on <u>Anterias ferboal</u> and tend to demonstrate the many ways in which a given response may be brought about in the vertous gam representatives of the retarpides. I have, more Dver, so far been unable to get in <u>Figoriar</u> the marked derep. flexion which have figures for far heights forbent. It would be obviously impossible for the suckers to attach, yet the animals (<u>Asterina</u> 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 ge 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, 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 c.

The righting reaction of <u>Asterina</u> on sand is even neater than that of <u>Pisaster</u>. 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.

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would be obviously impossible for the suckers to attach, yet the male (<u>Asterins</u> especially) righted themselves quite as neatly as a solid substrate. Fisaster, however, would not right easily un-

a in sotive locomotion at the time of inversion.

A specimen actively drawling in the direction of a c g. 16) was quickly inverted on sand. The tube feet, which were rected because the animal was lifted from the substrate, extended .e s brewet beselwt bas willsre qu bevon h bas E .e s brewet conc bas and over the disk while a ge twisted toward each other and tube feet, as soon as they came in contact with the sand, began "loss' tes of as os bevon ver dose suil The set its said edut (betabirg) bebasize viewites est of celens idsir is virsen e t. The stapping activity of the tube feet on a g resulted in their bling back under themselves, so that the tube feet were striking toward the disk instead of away from 12 (see rays, fig. 18, 19, 20). step reflexes of the tube feet in contact with the sand were yery -jape bus buss of the feet clouching back through the sand and soaterecentines out to eno to constall a of cebla fie no enters out pat beiles bad e a ever out fitau bountinos betsitiat audi ainemevom as' wader the disk and the other rays had moved up over the disk far ugh to overbalance the animal and complete the somersault. Loco-. e a lo molicerib ent al beunismon ment mol

The righting reaction of <u>Asterina</u> on sand is even neater n that of <u>Piecater</u>. This is due to the very great flexibility of ray time and to the strangth and size of the large disked tube t. The animal rights nearly as quickly and easily as on a solid strate.

INTERPRETATION OF THE RIGHTING READTION AS A PHASE

Syldenge from the movement of the tube feet and arms.

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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 (1) 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 (1910;1910b) Cole (1913 \triangleleft)) 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.95), 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.

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In general torus, the above interpretation is that the noisesneiro rieds to noisestlb eds at tuo bactue jest edus beseten an this state are ready to give the step reflex upon contact stimsafter ere ereal moltalumits fortheon dous to somends and al .nots guovies feresides ent bas disade ferrebous ent seevict soutos tem of such a nature that the ray, by twisting or banding or both edus beineiro vievisos edi os selgas idair se virsen eres ligeri s betreval ismins as to essense the first movements of an animal inverted test edut bebnette and to LLA .g & brewot not concool evites in. bas 91. .aght . remetae terror eas to active the at beburyong (), qg) vbsoris bediross as ans of the almost of straige (gp () virsen eron noitinog a gniswees yer out in the gnither at flueer : -org phisthir end antrol .jeel edus beinelro eds ditw eelans idgi: afismins out bravet bebreixe mismer teel edut beteindtenu ent t stior. The rays a s. however, is accordance with the above princibend toward one another and down so that the tube feet gome in rennem ont al bas zeffer gets out studenes, esertadue out dity tos. .aniddain end sisiainf evods bent.

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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.

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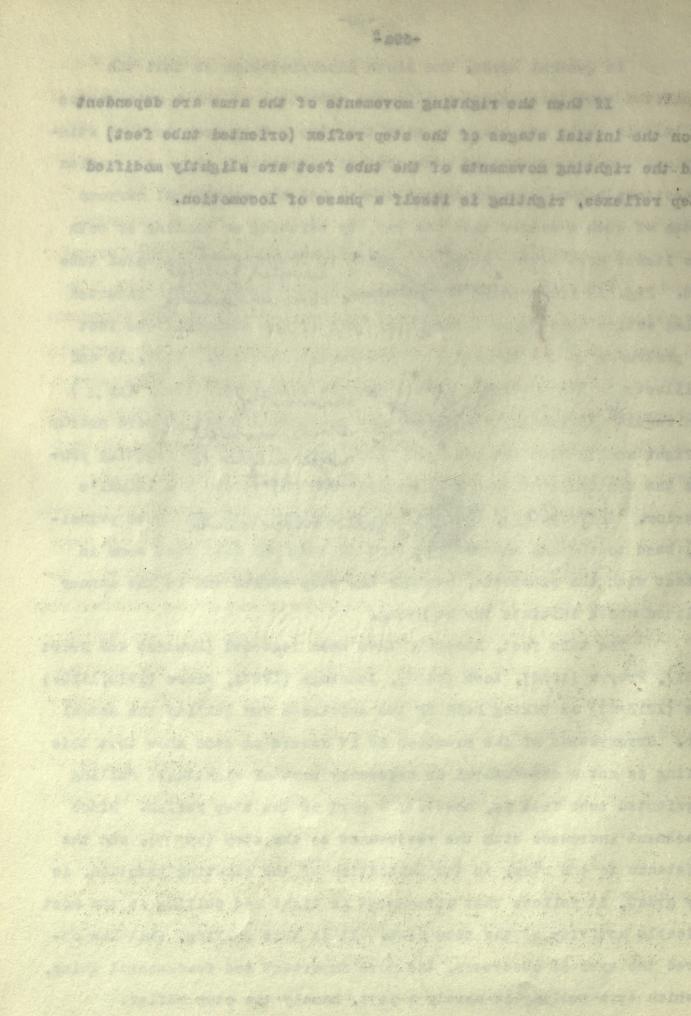
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starbish just showing coordination. movement of mo more at ght angles to le feet. er movements.

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Evidence from the fact that the stimulation of the doreal myodermal sheath of the ray is not an essential factor in 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 chows 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.

myp, my observations and the statements available in the literature

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Aridence from the fact that the stimulation of the dormal referred riverth of the reg is not an encential factoric the riverta

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If the righting readtion is simply a modification of ordinry losomotion. it would be expected first that contact stimulations is the dorest myodemnal aneath of the ray do not play an essential art in the ordinary locomption and second, that, since the locomotor add ,emit to signel enos to' not south nevie a at elaieved estuan notive noticostic a shore accounting a discussion anishal a very closely correlated with loomotion before and a they righting. blor al name as batels very werthe a state and la rever estably the stay is stay is and all other between beenelsd has no is once sector the bottom of a small inverted bester. Usra was taken all events of for box laib and vice denot of not clusters and a -mile transformer the water or subject then to any other unnecessary stimlation. In every case two or many of the rays started to band down THE W doreally while the rays on the equinte side began to bead up. not in venous were nore real than the rowner and the work with a con verbalanced and fall off the beaker. This was reparted as many times -ordnor has actually one doubt in any mind that due dorseflexion and rentrogativitate of the operation of the "unified impulse" gates ron the locanotion. That these movements are homologous with the soit bis ve beleeibal at (1 ages synthet) asneaves by the files hat the rays which turn down turn also, usually, toward cach other, a

A This conclusion is rendered more probable by the fact that one of the neurotomized starfies when coordinated in locomotion ould show righting movements if inverted guickly and gonily. These ovements were similar in direction to those of the normal animal at some complicated by the fact that seemer or later these animals ended to take the "taily form". (Romanes and Swart 1981). In a ev cases they righted theselves quice promptly.

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 fect 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 fect 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 <u>Astropecten</u>) than are mere dorsal flexures.

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Evidence from the persistence of the "unified impulse"

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Moore (1920) states that if suspended with the ventral side

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wn, an Asterias forbesi will remain motionless in a state of ne to ourt vistulosds fon elide while wished true of an tive Fiencher consolally at first, and very far from true of an tive Pronomodia, may be said to describe the behavior of the more active speciment that I have tried the experiment upon. Moore ye, furthermore, that if the doreal wall of a ray of such a susnded specimen be irritated by rubbing it with a glass rod, the y will flex derually. I have confirmed this. Moore, however, gleats to mention a fact, first observed, by Romanes and Ewart (1881) at the tube feet of such a ray whose dereal dennis is irritated as no seal edut to noiseinsito Leanon edt .vivitos at essero thre but unoriented speciman is powerd the tip of the rey. It would en then that the dereal flexure is due to the principle that a ray -to vievities and of seight is virter eron liest ise of abn thing a sa eldstance arom out ansared at stuff .teot adut beta of bevreedo need and feet but the tild loss and eonie wely read to the tube feet of other tays and to be followed by doreal vements or lateral twistings of these other rays. "No relimie bus each wort apleulones out of semos ered and on doldy ever but to services? Learob end that examin edi to sivad eterages and are egotisfumlie icednos yd beilol notioner anitheir out test tost out mort oblad . noticer pairing add to moidsiumize desince what such a train of bevreedo meed a ye, my observations and the statements available in the intersture we led me to the conclusion that lateral twistings of the mays to fail even anticeser anitabir end at instrogat even four et .serurell iserob even eve mad (motoegori "selucation 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 (1913) 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 arguesas 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	0	ed	d	de	e	ea	a a'	b b	be
Crawling previous to test	2	6	5	1		REC .	3	2	
used in righting		3			2	16		1	2
orawling subsequently	2	9	5	1			2		3

This shows that whereas the four speciments used in these tests righted themselves on arms <u>e a</u> 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 <u>e</u> 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 <u>e</u>, 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

-72-

It remains now to inquire into the correlation between the

rection of righting and that of Locomotion before and after the lation. Cole (1913) has presented some evidence on this point. from in he draws mersilve conclusions. Els analysis of the data is, I he, incomplete and the data are not statistically representative. He arguéses follows.

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"In table 4 are shown the results of a number of tests to comine minat relation exists between the arms used in righting when a starfish is placed on its aboral surface and the direction of lonotion previous to and subsequent to the righting reaction. The

Arms Arms be a cold of the constant of the c

chted themeelves on arms <u>a A</u> sixteen out of twenty-four times, they a been in nearly all cases orawling in a direction nearly opposed these arms, and moreover they continued locomotion in the same neral direction after righting themselves. An examination of the tividual records reveals the same relations in a great majority of eas."

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hed to help in interpreting the data. Gole's studies have led a to the conclusion that the starfish studied orawls with g anterr, more than with any other rays anterior. Unfortunately, however, these experiments he chose animals that were not typical in this spect, since in no trials were they erawling toward g, and in all tour trials were crawling in a very different direction. This in anection with the fact that only four speciments were used, all

froenth us Suffaces

-Table 4-

-73-

Relation of arms used in frighting to direction of

previous and subsequent crawling.

.4	Individual After trial 50#	Previously crawling anterior	in righting	physiolo-	Subsequently crawled anterior	Shift of anterior from "pre- viously orawling" (rays)
.4	After trial 50#	d	ea	1.5		
10	Before " 1#	10 000 Can 20	ea	Semilar dr	our tas	moy the
10	Agter " 10# After " 16#	er cightin	e(b)	2	ed. be	2.5
lo	After " 28#	ed	ea	2	cd	•5
10	following day	1612 BOC	d	0100.012.000 52.000	ba	
20	H 10 montrie	a	be d	t of 2.5	or a derring	1.5
1.2	Trial 1	**	be	A00	a a a a a a a a a a a a a a a a a a a	
12	a zzya used i	antes	ca	of 3.5 101	de	1.5
22 2	" 3 " (Alee como)	de cd	ab int,	hour is	od us an	.5 right
22	* 5	C	ea	2.5	od	.5
14	" il a direa	then adaptly	ea		g and an and a	
14	H Zenels (a)	d distance	a tolea corere	1.5 1.5 ut	thed and these to	.5
14	. 4	cd	ea		od	s) 0
4	P (5 2 Carpension)	cd	ea		od	
4	" got sh h	cd	ea ea	2 1.5	ondately ag	.5
14	" 8	d	ea	1.5	od	.5
14	· 90 /2120	od	ed ed	1 0010 miles	stationary	
14	" 10 " 11	be	ea da taile	d amplinati	en od delde	data doss
-	the second s	นของกลางสีวิธีชื่อการคางคุณสุดของสุด	nan depending die seine andere eine	างสารสองสะเสราะที่เรื่องการการการการสารส		the difference in the second second

rage

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

fire experiments serve made of the territy well starfish (80

(include and a Antonica). The starlish used ware in addive

is meaning except in case of going of the Asterina as enous in

the property residuation may as gettle as possible; the animal

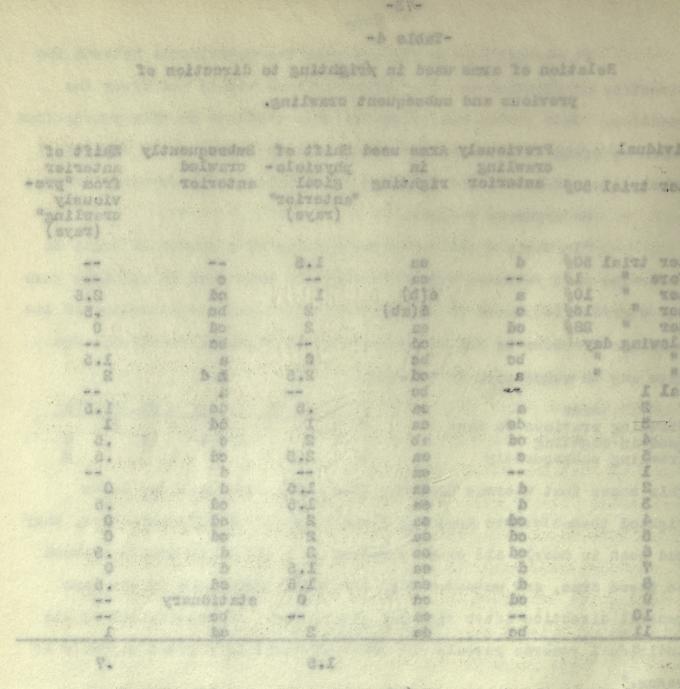
Diversive Sectors in the surroundings such as light of areas of

sundley stars were mainted by rotating the animal in successive

bain picked up by the disk and inverted quickly without, in

most errow, hirting is abeve the surface of the water.

BALL ZANGE THE RELATIONS DESCRIPTION



trials were of a series of 450 showing the permissers of the gloal enterier in a general direction, which tends to rotate a the right or the left.

direction of locomotion, leads me to believe that the data 15 are not a good foundation for any conclusion. Moreover the they ao conclusion it does indicate is not that drawn by Cole.

As seen from an examination of column 5, the 17 records show that the Physiclogical anterior has shifted in one direction or the other andverage 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 Vefore) 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) erawling. But the arithmetical difference between these averages of data $(1.5 - .7^{\pm}.8)$ 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 antorior and the arms used in righting seventyfive experiments were made with twenty-six starfish (20 <u>Pisaster</u> and 6 <u>Asterina</u>). 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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-74-

direction of locanotion, leads as to believe the the date 25 of are a good foundation for any conclusion. Experse the Gonolusion it for to have seen from an examination of column 5. the 17 recercin atour that the Experiological anterior has sufficien in one direction or the other anavarage of seven tenths of an inter relation, per recetion. Goles conclusion on this point, as even above is that "they" (he sheftish) continued to erand, in the same general direction (as they file point after righting General real and a the file of the first of the continued to erand, in the same general direction (as they file point after righting General real.

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horeever, as seen from an examination of bolumn 3, the 19 records show an average shift of anterior (referring to the rape used to right as anterior) of 1.5 inter radii per resolten. (ales condinated on this point, however is that the sainals right in a direction boardy ergouile to that in which the sainals right viously (and subsequently) ergeling. But the srithmatical difference between these everages of date (1.5 - .72 .8) is the shift (.7 interrative) which to be regards in a provide to all. Obviously, then a fatalise state of the regards is no shift at all. Obviously, then a fatalise state of the test and the shift of all. Obviously, then a fatalise state of the state of the scale of all. Obviously, then a fatalise state of the state of the scale of the shift (.7 interrative) which the same state of the scale of the shift optimate of an allowed as and the state of the scale of the shift of the same of the scale of the scale of the scale of the shift of the same of the scale of the scale of the scale of the scale of all. Obviously, then a fatalised examination of foles date does date does , not confirm bie conclusion.

With an idea of clearing up he relationship between the physiclogical autorior and the arms used in righting sevenyfive experiments were made with tranig-aix starfiel (20 <u>Elegater</u> and 6 <u>Asteriar</u>). The starfieh used were in active locametion, except in case of some of the asteriae as shown in the record. Manipulation was as gentle as possible, the animal being piezed up by the disk and inverted quickly without, in affect asses, lifting it shows the surface of the water. Directive factors in the surroundings such as highle or areas of another store, were excluded by rotating the animal in successed wither.

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

dividual.	Direction	first	Shift	Arms bent	Arms righted	Shift	Direction after	Shift of
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aster o #	a0	aed	0.0	bc ed	ed	1.0	0	0.5
5 11	ae ae	aeb	0.0	bc	ab	0.5	ed	1.0
2 "	de	6	0.5	(a)bod	la)e	1.0	20	1.0
1 "	0	2(0)	0.5	-	ae	0.5	ae	0.5
2 #	de	dea	0.0	bc	d	0.5	od	1.0
4 11	2	(a)bod	0.0	bo				
5 *	de	de(c)	0.0	be	de	00	ao	1.0
5 #	6	ae(d)	0.5	bo	a(d)e	0.5	8	0.0
5 ¹¹ 5 ¹¹	20	a(b)de bc	1.0	c(b) a	de bc	1.0	d be	1.5
0	b	be	0.5	dea	be	0.5	C	1.0
5 # 5 #	80	eda	1.0	bc(d)	ae	0.0	30	0.0
17 11	e	ae	0.5	bod	ea	0.5	63	0.5
8 11	bc	(b) c(ad		(b) mst	bá	1.0	cđ	1.0
8 #	de	de	0.0	-	de	0.0	a	0.5
7 11	cd	b	1.5	acde	6	1.5	b	1.5
5 11	de	de(c)	0.0	bea	de	0.0	de	0.0
	ae	e(a)b	0.0	(b) od	20	0.0	26	0.0
5 n 9 n	a 	(b)ae abcd(e)	0.5	bo	ae ab	2.0	stopped	
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10 "		bc(a)	0.0				-	
11 "		be	0.0	ade	bo	00	be	00
7 "		cd	0.0	abe	cd	0.0	14	
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12 "		dec	1.0	ab	de ae	1.0	de	0.5
12 "	de de	(a)de e(all)a	0.0	bcd	ea la	1.0	Ga	1.0
12 "		ed	1.0	ab	ed	1.0	ed	1.0
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16 "		a	2.5	(e)(a)bed		2.0	ae	2.0
16 "		ae	0.0		ae	0.0	20	0.0
16 "		ed	1.0	cba	ed	1.0	Uc	2.0
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16 "		ac	0.0	bed aed	ae be	0.0	lic	0.0
17 "		be be	0.0	aed	be	0.0	be	0.0
17 *		be	0.0	acd	bo	0.0	bo	0.0
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19,"		abode	**	(dea)	bc	1.5	od	0.0 5
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Relation of arms used in righting. to direction of provieus and subsequent orevites.

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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 (maps 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 Cold's data shows that careful manipulation of the starfish and the use of a large number of individuals riduces 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 back toward 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

-75-

Hoderds ware taken (column 1.) of the direction of lowenstion before righting and (column 2) the area that, after inverting, the animal, first buigted and beat down toward the substrate. These two findings were convered in and experiment and the shift in atther direction of the laiding rays or "physiclogical anterior" set down in column 3. The turning down of cortain rays is usually followed (many or preseded) by a lifting up of others. The rays that lifted up free of the substrate + but not these , over boditesto yew ent al , et erisadue out ao betnelto erew sant to walk over the initiation rays, were now yeared (column 6). The rays that turned down whro not, slowys, of course the ante as these that the animal uses in righting. These latter are listed in column 5, and the shift of abteutor from the direction before inverting to the area used in vichting is Linked in column size. The anterior ofter righting is listed in al phistoval etcled antically and from the direction before inverting is Listed in column 8. Thus the shifts of anterior, listed in columna 5,6 and 8 refer to the original adtains before inverting. A secontion of the averages obtained here, and the social the trops Cold's data shows that saveful manipulation of the starfish and the use of a large number of individuals riduces the shift or anterior considerably. As shown by the rays that are first turned down, the anterior at the beginning of righting has .nusidevreede 28 lo energys us no subber-woint no lo 88. hettide As shown by the rays on which the animal rights, the anterior more subbar-rotal as to 3. batting and acligate galddare dat galaub where it was before the animal was inverted. After rightles, the an instabuld Innihito all brevel ford ultrails efficie terretan shown by the fact the average shift after rightne is less tions during righting. This shows more markedly in the average

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drawn from Cole's table.

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.

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Cole (1913) has shown very conclusively that the impulse to locomote, in the starfish tends the 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 eount Occurring quite frequently. In a commuting up these deviations (cole) from the table opposite p. 16 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, . 67/ interradii)obtained from the status of the direction of the coordinated impulse throughout the righting reaction.

I conclude therefore that righting is an aspect of locomotion.

drawn from Cold's table. te an example of the teadency which we have noticed in connece. tion will the seviation reaction (p. 57) for the coordinated inpulse to return to its original direction, even after having head actively orisoled in some other direction. Gala (1913) has anown very conclusively that the impulse to locompts, in the stariish tends is no anistain the same and felti dise desviol). Inits of faits mort , noticento istanon has becout one intervented by the disk barris the rege drapped and evidentian on the bottom of an aquarian in a non-directive dismber.]. 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 above dovisions, of iven one half to two and a half inter-radi emold streb ensit on unlansed genurting out to frequently. 27 32I from the table appendix of the hermone verid and thurst environ to a guan to tak of 217 inter-which in 499 triging. this amounts the estur at metals forst and liber-redul 51. To valuadas to dilus a "Total 178. 00., 80.) countr and do he wise it estimates a der some beforlived from the statue of the direction of the coordinated incloses throughout the righting reaction. I conclude therefore that righting is an angeot of loosetien.

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1/ <u>Pisaster ocraceus</u> 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 the 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 a tached with 2.8 (<u>Asterina</u>) or 2.06 (<u>Fyonopodia</u>) 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 feflex 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 ref rable hypothetically to a simple nerve net.

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b) The step rofies interpreted with the set withdrewal response as eligited by contact stimulation of the emouleoral disk. (t) is dependent upon the contact stimulation and the pressure of the indent of the be rigid and support bained 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 (<u>Autoring</u>) or 2.06 (<u>Evenopodis</u>) times as much force as it exerts in public square traistance. The frace is strongly during boundant values of the resistance. The frace is relatively constant for various ratios of the resistance. The frace is strongly of the store is reflex against resistance. The frace is strongly of the store is reflex values of the resistance. The frace is strongly of the store is reflex actions markedly with different spectrum.

S/Coordination of the tube feet of the rigid starfish, like that of the gills, is a simple spread of extension or retroction. It is ref rable hypothesically 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 (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.

11/ The righting reaction is a phase of ordinary locomotion

7/ Coordination in the active but unorianted 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 sutotomy.
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11/ The righting reaction is a phase of ordinary locomotion

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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 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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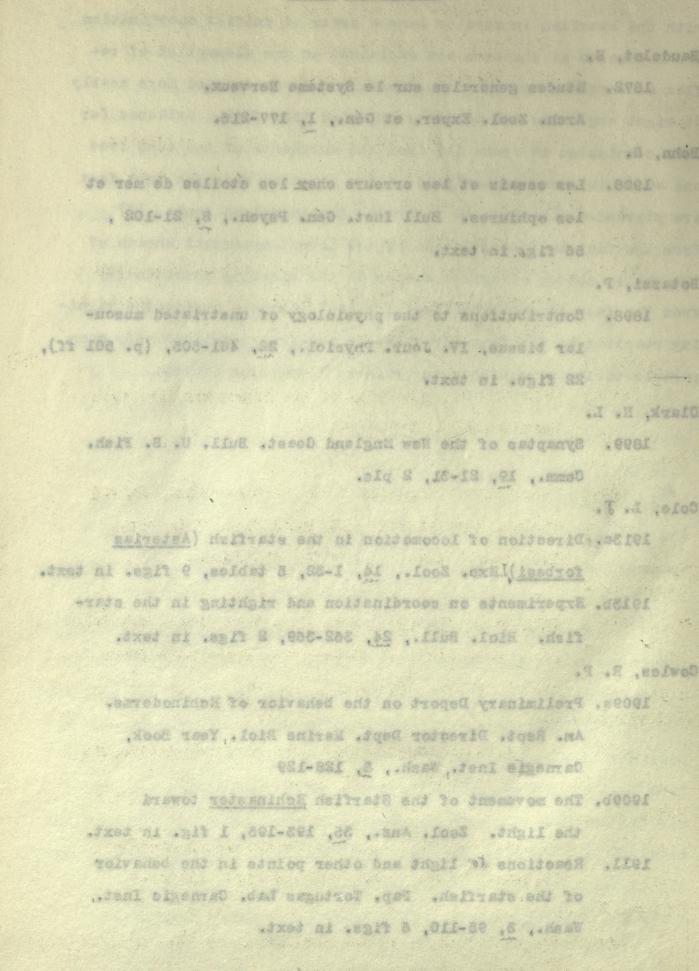
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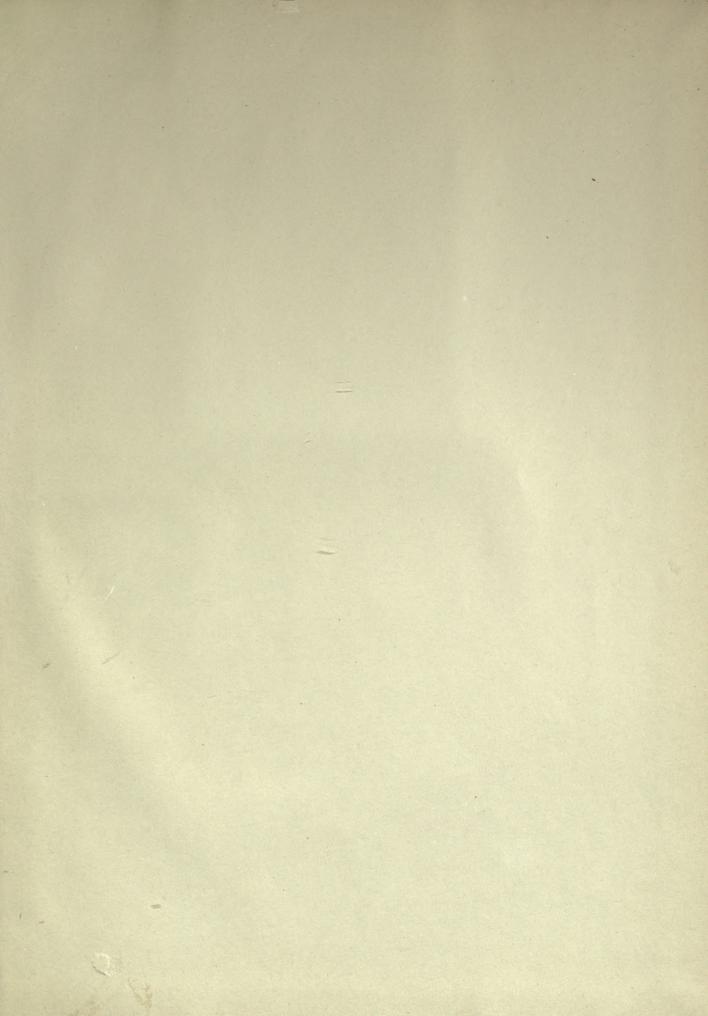
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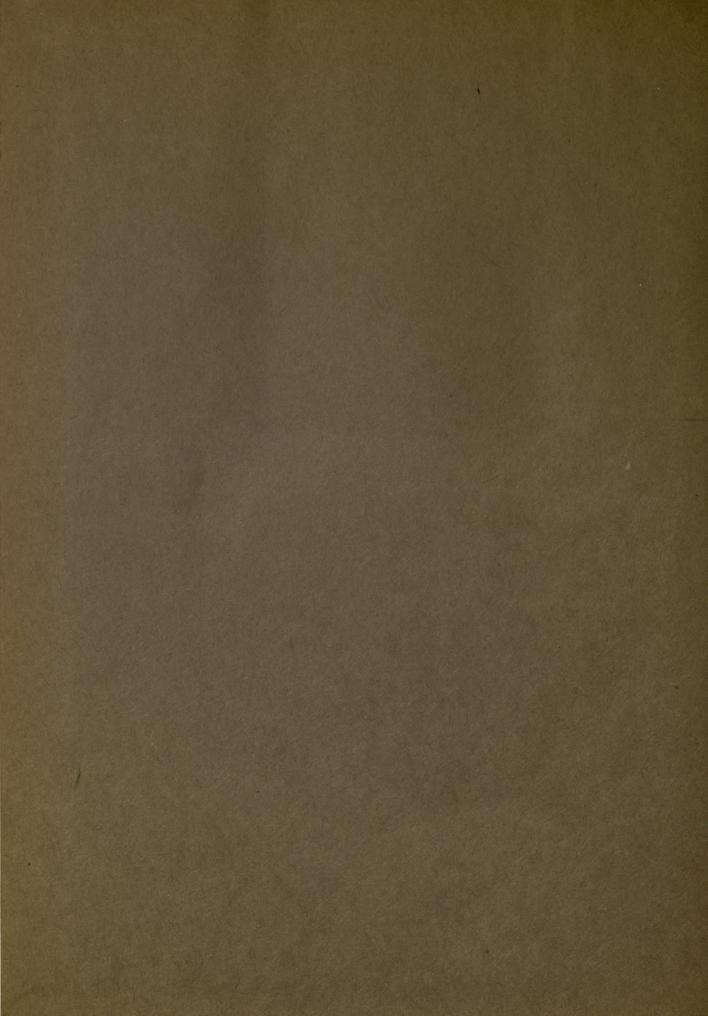
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