VII. *Concluding Observations on the Locomotor System of Medusæ.*
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In my previous papers on this subject the considerations are sufficiently explained which originally induced me to defer any systematic investigation concerning the histology of the Medusæ, until the more important of the physiological observations should have been completed. While preparing the material for these papers, I was not blind to the fact that it served still further to ripen the promise that a careful development of the histology of the Medusæ would prove highly remunerative in morphological results. But I felt that, even if no other workers should enter the field from the side of morphology, it was more desirable that the physiology of these primitive nervous tissues should be speedily worked out than that their structural peculiarities should be so. Whether or not this view was a wise one, in the result it has proved beneficial; for not only was I fortunate enough to procure the co-operation of so competent an histologist as my friend Mr. Schäfer in working out the histology of the covered-eyed Medusæ, but contemporaneously with his researches there was also being carried on by Messrs. O. and R. Hertwig a most painstaking and thorough investigation of the histology of the naked-eyed Medusæ. At the same time, also, Professor Eimer had been continuing his microscopical researches. In this way, therefore, both the physiology and the morphology of the Medusæ were simultaneously worked out in parallel lines, with the result of furnishing a much larger and more complete body of information than could possibly have been obtained by a single observer in double the time.

Of Professor Eimer's microscopical work it would be now premature to speak, for as yet he has only published a somewhat meagre abstract, with the promise, however, of shortly supplementing it with a more complete and detailed exposition. Of Mr. Schäfer's work I have previously spoken in the highest terms, and before the present remarks will be in print the Fellows of the Royal Society will themselves be in a position to appreciate its merits. Of Messrs. Hertwig's work it is difficult to speak without enthusiasm; but as I shall conclude this paper with a brief *résumé* of the present literature on the morphology of the Medusæ, it is needless that I should here dwell on this, the most meritorious of its existing memoirs.

Understanding that Mr. Schäfer is still prosecuting his investigations, and observ-

ing that the last-mentioned memoir is of so masterly a character, I have this year thought it desirable to abandon my original intention of concluding this series of papers with the results of a systematic investigation of the histology of the Medusæ. Entertaining not the smallest doubt as to the accuracy of the results which have been obtained by the laborious inquiry of Messrs. HERTWIG, I felt that time would be more profitably employed in extending the lines of my physiological researches than in con-firming morphological work which, to my mind, did not stand in need of confirmation. Feeling thus that the histology of the Medusæ in all its leading features had been, relatively speaking, exhausted, I this year devoted myself to continuing and con-cluding the physiological work with which I began. I may observe, however, that when opportunity again permits, I hope to investigate the histology of those species of naked-eyed Medusæ on which I have mainly experimented; for with the exception of *Sarsia*, these particular species have not as yet been submitted to microscopical exami-nation by any of the more recent observers. Should this investigation tend to show that the nervous tissues of these particular species present any peculiarities which have not been described as occurring in the numerous species of naked-eyed Medusæ which have been so carefully examined by Messrs. HERTWIG, I shall communicate the results of my investigation in a supplementary paper to the Royal Society. But meanwhile I communicate this additional instalment of physiological results under the title " Concluding Observations on the Locomotor System of Medusæ." Possibly enough in future years various questions concerning the physiology of nerve and muscle may arise, for the solution of which the primitive nerve and muscle tissues of the Medusæ will afford valuable material; but for the present, it seems to me, this paper will pretty well exhaust the physiology of these tissues, and for this reason I have given it a title which indicates that the series of communications of which it is a member may now be considered as closed.*

I. STIMULATION.

§ 1. *Artificial Rhythm.*—(*a.*) I shall devote the whole of this lengthy section to a full consideration of what in my previous paper I termed " Artificial Rhythm." It will be remembered that in my previous paper this subject was alluded to in a foot-note, of which the following is a copy:—" As the present communication was originally accepted by the Royal Society, there here followed a lengthy subsection on ' Artificial Rhythm.' A condensed epitome of the main facts which were detailed in that sub-section may be found in the already published abstract of this paper in the ' Pro-ceedings of the Royal Society.' But as the new theory of ganglionic action, which it is the main object of this passage to disclose, appears to me a theory of sufficient

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* The effects of several poisons still remain to be investigated, and I have still in view a number of experiments which have not yet been carried out; but as it is uncertain whether the results of these further observations will be worth publishing, I have thought it desirable thus to indicate that the work, so far as it has now gone, may be regarded as a completed structure.

importance to demand its final publication in as complete a form as possible, I have sought and obtained the permission of the Royal Society to withdraw this subsection from the proof. . . . . The facts of which it treats form in themselves a connected body distinct from all the other facts which are detailed in the rest of this communication; so that, while their omission from the present paper does not entail any furthur modification of the latter, they will admit of being introduced *en masse* in my next paper. When, therefore, I shall have completed the further experiments which in this connexion I have devised, I shall hope to communicate to the Royal Society, in a single connected series, all the facts and inferences which bear upon this subject."

Although I have not even yet completed all the experiments which it is desirable to make with reference to this subject, I have this year so far added to their number that I feel the research is now sufficiently ripe for publication. As already stated, an epitome of the main facts regarding artificial rhythm has previously appeared in the 'Proceedings of the Royal Society'; but of course it will now be necessary to give a more detailed account of these facts, no less than of those which I have more recently observed. Stating, then, all the facts as concisely as possible, they are as follows.

(*b.*) If the umbrella of *Aurelia aurita* has been paralyzed by the removal of its lithocysts, and if it is then subjected to faradaic stimulation of minimal intensity, the response which it gives is not tetanic, but rhythmic. The rate of this artificial rhythm varies in different specimens, but the limits of variation are always within those which are observed by the natural rhythm of different specimens. The artificial rhythm is not in every case strictly regular; but by carefully adjusting the strength of the current, and by shifting the electrodes from one part of the tissue to another until the most appropriate part is ascertained, the artificial rhythm admits in most cases of being rendered tolerably regular, and in many cases as strictly regular as is the natural rhythm of the animal. To show this, I append a tracing of the artificial rhythm, which may be taken as a fair sample of the most perfect regularity that can be obtained by minimal faradaic stimulation.*

Fig. 1.
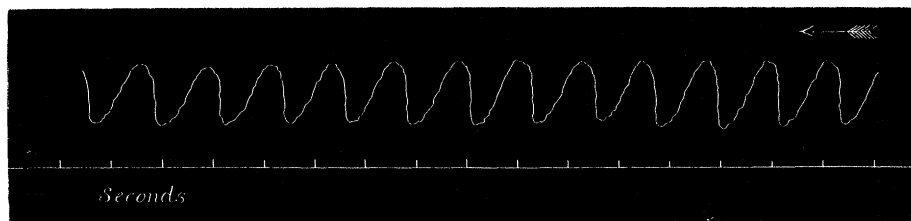
This artificial rhythm may be obtained with a portion of irritable tissue of any size, and whether a large or a small piece of the tissue employed be included between the electrodes.

* This and all the subsequent tracings I obtained by the method already described in my previous paper.

(c.) As the fact of this wonderfully rhythmic response to faradaic irritation was quite unexpected by me, and as it seemed to be a fact of great significance, I was led to investigate it in as many of its bearings as time permitted. First, I tried the effect on the rhythm of progressively intensifying the strength of the faradaic current. I found that with each increment of the current the rate of the rhythm was increased; and this up to the point at which the rhythm began to pass into tetanus due to summation of the successive contractions. But between the slowest rhythm obtainable by minimal stimulation and the most rapid rhythm obtainable before the appearance of tetanus, there were numerous degrees of rate to be observed. I here append another tracing to show the effect on the rate of the rhythm of alterations in the strength of the current (fig. 2).

Fig. 2.
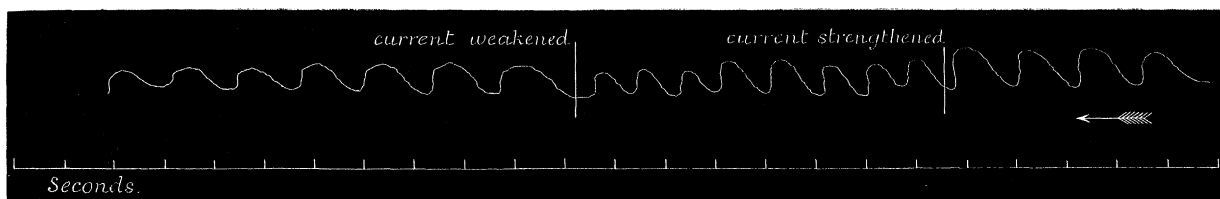
It will also be observed from this tracing that, in consequence of the current having been strengthened slightly beyond the limit within which strictly rhythmic response was attainable, the curves in the middle part of the tracing, where the current was strengthened, are slightly irregular. This irregularity is of course due to the first appearance of tumultuous tetanus. If the faradaic stimulation had in this case been progressively made still stronger, the irregularity would have become still more pronounced up to a certain point, when it would gradually have begun to pass into more persistent tetanus. But as in this case, instead of strengthening the current still further, I again weakened it to its original intensity, the rhythm immediately returned to its original rate and regularity.

(d.) The next point I investigated was the persistency of any given rate of rhythm under faradaic stimulation of constant intensity. I found this persistency to vary with the vigour of the specimens experimented on, as well as with other conditions which I need not wait to specify; but in all cases the persistency was much greater than I had expected. For the sake of brevity I shall confine myself in this connexion to giving the particulars of one experiment. A detached quadrant of *Aurelia,* whose normal rate of rhythm was 18 per minute, had its lithocysts removed, and then formed the subject of the experiment. The faradaic stimulation supplied to it was of slightly more than minimal intensity, and the resulting rhythm was perfectly regular at the rate of 38 per minute. This absolutely perfect rhythm continued, without once faltering or changing its rate, for an hour and a quarter (tracing, fig. 1). At the end of this time single omissions in the series of contractions began to occur at long intervals—*i.e.,* after every one or two hundred rhythmic contractions, a short pause

would occur of a length equal to the time occupied by a single contraction. These omissions then gradually became more and more frequent, till finally they gave rise to well-marked irregularity (tracing, fig. 3). Shortly afterwards all movements entirely

Fig. 3.

Seconds.
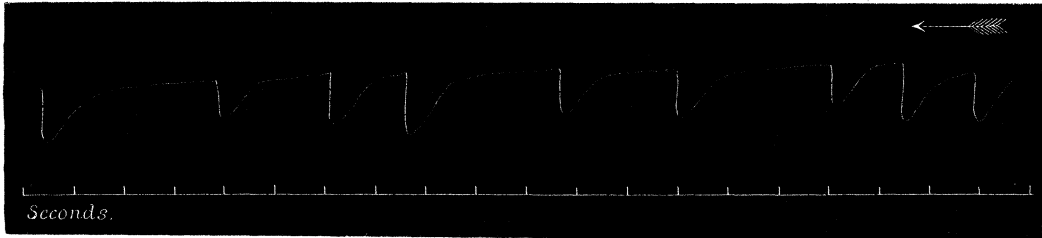
ceased, and failed to be aroused even by strengthening the current. This cessation of response through exhaustion took place rather more than an hour and a half after the first commencement of stimulation. I then allowed the tissue to remain quiescent for fifteen minutes, and again stimulated, but no response was given. After the lapse of a further fifteen minutes response was given to the faradising current at the moment of its closure, but not during its passage. I now gave the tissue another quarter of an hour's rest, and then obtained responses to faradisation of a partly rhythmic nature. Lastly, on waiting for another quarter of an hour—*i.e.*, one hour from the time at which the persistent stimulation for an hour and a half had ceased—the movements in response to faradisation were strictly rhythmic, although for the same strength of current the rate of their rhythm was now slower than before—viz. : 28 per minute. (But on placing another pair of electrodes on another part of the tissue, the original rate of 38 per minute could be obtained.) I now again persistently tetanised for an hour, and throughout that time obtained perfectly regular and sustained rhythm of 28 per minute. Exhaustion had not again supervened when the observation terminated.

(e.) Such being the facts, the question arises as to their interpretation. At first I was naturally inclined to suppose that the artificial rhythm was due to a periodic variation in the strength of the stimulus, caused by some slight breach of contact between the terminals and the tissue on each contraction of the latter. This supposition, of course, would divest the phenomena in question of all physiological meaning, and I therefore took pains in the first instance to exclude it. This I did in two ways : first, by observing that in many cases (and especially in *Cyanæa capillata*) the rate of the rhythm is so slow that the contractions do not follow one another till a considerable interval of total relaxation has intervened; and second, by placing the terminals close together so as to include only a small piece of tissue between them, and then firmly pinning the tissue all round the electrodes to a piece of wood placed beneath the Medusa. In this way the small portion of tissue which served as the seat of stimulation was itself prevented from moving, and therefore the rhythmic motions

which the rest of the Medusa presented cannot have been due to any variations in the quality of the contact between the electrodes and this stationary seat of stimulation.

(_f._) Any such merely mechanical source of fallacy being thus, I think, excluded, we are compelled to regard the facts of artificial rhythm as of a purely physiological kind. The question, therefore, as to the explanation of these facts becomes one of the highest interest, and the hypothesis which I have framed to answer it is as follows. Every time the tissue contracts it must as a consequence suffer a certain amount of exhaustion, and therefore must become slightly less sensitive to stimulation than it was before. After a time, however, the exhaustion will pass away, and the original degree of sensitiveness will thereupon return. Now the intensity of faradaic stimulation which is alone capable of producing rhythmic response, is either minimal, or but slightly more than minimal, in relation to the sensitiveness of the tissue when fresh. Consequently when the degree of this sensitiveness is somewhat lowered by temporary exhaustion, the intensity of the stimulation becomes somewhat less than minimal in relation to this lower degree of sensitiveness. The tissue, therefore, fails to perceive the presence of the stimulus, and consequently fails to respond. But so soon as the exhaustion is completely recovered from, so soon will the tissue again perceive the presence of the stimulus ; it will therefore again respond, again become temporarily exhausted, again fail to perceive the presence of the stimulus, and again become temporarily quiescent. Now it is obvious that, if this process occurs once, it may occur an indefinite number of times ; and as the conditions of nutrition, as well as those of stimulation, remain constant, it is manifest that the responses may thus become periodic.

(_g._) In order to test the truth of this hypothesis, I made the following experiments. Having first noted the rate of the rhythm under faradaic stimulation of minimal intensity, without shifting the electrodes or altering the intensity of the current, I discarded the faradaic stimulation, and substituted for it single induction shocks thrown in with a key. I found, as I had hoped, that the maximum number of these single shocks which I could thus throw in in a given time, _so as to procure a response to every shock_, corresponded with the number of contractions which the tissue had previously given during a similar interval of time when under the influence of the faradaic current of similar intensity. To make this quite clear I shall describe the whole course of one such experiment. The deganglionated tissue under the influence of minimal faradaic stimulation manifested a perfectly regular rhythm of thirty contractions per minute, or one contraction in every two seconds. While the position of the platinum electrodes and the intensity of the current remained unchanged, single induction shocks were now administered with a key at any intervals which might be desired. It was found that if these single induction stimuli were administered at regular intervals of two seconds or more, the tissue responded to every stimulus ; but that if the stimuli were thrown in more rapidly than this, the tissue did not respond to every stimulus, but only to those that were separated from one another

by an interval of at least two seconds' duration. Thus, for instance, if the shocks were thrown in at the rate of one a second, the tissue only, but always, responded to every alternate shock. And similarly, as just stated, if any number of shocks were thrown in, the tissue only responded once in every two seconds. Now, as this rate of response precisely coincided with the rate of rhythm previously shown by the same tissue under the influence of faradaic stimulation of the same intensity, the experiment tended to verify the hypothesis which it was designed to test.

(h.) But in order to test this hypothesis still more effectually, I conducted a number of experiments on a slightly different plan. As already stated, the intensity of the faradaic stimulation has a marked influence on the rate of the rhythm, up to the point at which the rhythmic effect of such stimulation begins to become lost in the tetanic effect. Well, by choosing at random any strength of faradaic stimulation between the limits where rhythmic response occurred, and by noting the rate of the rhythm under that strength of stimulation, I found that I was generally able to predict the precise number of single induction-shocks which I could afterwards afford to throw in with the same strength of current, so as to procure a response to every shock—this number, of course, corresponding with the rate of the rhythm previously manifested under the faradaic stimulation. I say "generally," because this experiment was not invariably successful—any more, I may add, than was the first-mentioned and almost identical experiment in which minimal stimulation was employed (see paragraph g). Nevertheless, the exceptions were but slight, and always on the side of somewhat fewer contractions occurring in a given time in response to the single shocks than in response to faradaic stimulation. And as this is the direction in which we should expect, from the principle of the summation of stimuli, that slight deviations from the ordinary rule would occur, if they occurred at all, I do not think that the fact of their occurrence tends to impair the confirmation which these experiments certainly afford to the hypothesis we are considering.

(i.) Indeed, it seems to me that this hypothesis is so fully substantiated by these experiments, that I feel it is almost superfluous to adduce another experiment having the same tendency. Nevertheless, as the facts which the hypothesis is intended to explain are facts of considerable importance in themselves, and as the hypothesis in question will be shortly employed as tending to further the theory of ganglionic action in general, it is desirable that I should state all the experiments by which I have hitherto endeavoured to test it.

The experiment which I am about to describe cannot be understood without a preliminary account of certain properties of the contractile tissues of *Aurelia*, which as yet I have not described. The properties in question all appear to arise from the following fact—namely, that the contractile tissue admits of great variations in the vigour of its contractions. In my last paper, while treating of the summation of stimuli, it was fully explained that the force of responsive contraction in *Aurelia* varies greatly in the different parts of a "staircase" series; but quite apart from this

principle of the summation of stimuli, enormous variations in the force of contraction may often be observed under the influence of stimuli of varying intensities. This relation, within certain limits, between the intensity of a stimulus and the force of the responding contraction, is, of course, to be observed more or less in the case of all excitable tissues; but in the case of the excitable tissues of *Aurelia* the limits of variation in this respect are extreme. As it will be necessary to discuss this subject at length in the next division of the present paper, it will be sufficient in this place merely to state the principal fact, viz. : that the excitable tissues of *Aurelia* admit of giving either a very strong or a very weak response according to the intensity of the stimulus in relation to the excitability of the tissue. In view of this fact it occurred to me that a valuable means was afforded of testing the hypothesis whereby I had sought to explain the phenomena of artificial rhythm. For, if this hypothesis were sound, we might expect that by employing single stimuli of uniform and slightly more than minimal intensity, and by throwing them in at a rate slightly more rapid than is required to produce a strong response to every stimulus, the strong responses would alternate with weak responses. For after the occurrence of each strong response the restoration of excitability (or recovery from exhaustion) must be a gradual process, so that if the stimulus is thrown in when this restoration has proceeded to a certain, though not to its full extent, the stimulus ought to be strong enough to evoke a feeble response. This feeble response, however, would not greatly exhaust the tissue, so that when the next stimulus is thrown in it would encounter a tissue more excitable than did its predecessor, and consequently would give rise not to a weak contraction, but to a strong one. In order to test this idea I selected a specimen of *Aurelia* which exhibited marked differences in the strength of its contractile waves under the influence of stimuli of different intensities. Employing single induction shocks of slightly more than minimal intensity, and throwing them in at twice the rate that was required to produce a strong response to every shock, I found that midway between every two strong responses there was a weak response. In other words, a stimulus of uniform intensity gives rise alternately to a strong and to a weak contraction, as shown in the appended tracing. It will be observed that in this tracing each large curve represents

Fig. 4.
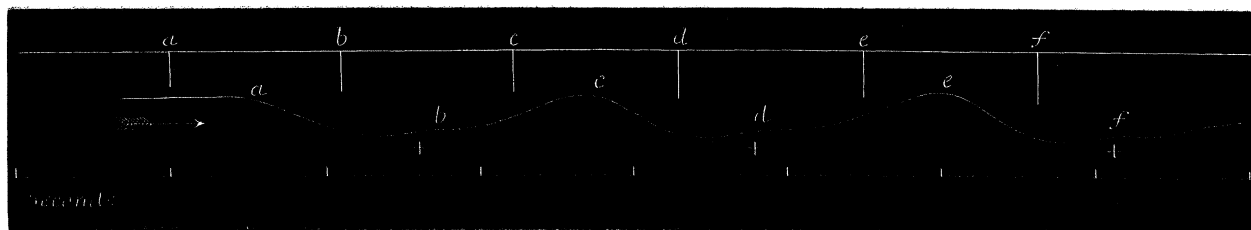
the whole time occupied by the strong contraction, the latter beginning at the highest point of the curve on the left hand side in each case. The effect of the weak contraction is that of momentarily interrupting the even sweep of diastole after the

strong contraction, and therefore the result on the tracing is a slight depression in the otherwise even curve of ascent. Lest any doubt should arise from the smallness of the curves representing the weak contractions that the former are in some way accidental, I may draw attention to the fact that the period of latent stimulation is the same in the case of all the curves. To render this apparent I have placed marks below the smaller curves, which show in each case the exact point where the depressing effect of these smaller curves on the ascending sweeps of the larger curves first become apparent, *i.e.*, the point at which the feeble contraction begins. Now, what I wish to be gathered from the whole tracing is this : If the strength of the induction shocks had been much greater than it was, *all* the contractions would have become strong contractions, and tetanus would have been the result. But, as the strength of the induction shocks was only slightly more than minimal, the exhaustion consequent on every strong contraction so far diminished the irritability of the tissue that when, during the process of relaxation, another shock *of the same intensity* was thrown in, the stimulus was only strong enough, in relation to the diminished irritability of the partly recovered tissue, to cause a feeble contraction. And these facts tend still further to substantiate the hypothesis whereby I have sought to explain the phenomena of artificial rhythm.

(*j.*) Upon the whole, then, I think that this hypothesis may be properly accepted as a full explanation of the artificial rhythm ; but whether or not the hypothesis is thus accepted, the facts which it is adduced to account for remain as remarkable and significant as they were before. That these facts are remarkable no one will dispute ; the degree of their significance will depend on the degree in which the inferences I draw from them appear to other physiologists of the same legitimate character as they appear to myself. These inferences will perhaps be considered somewhat bold, as they certainly must be considered premature ; and were it not that I think physiology may gain, while it cannot lose, from healthy speculation on such facts as those which are now before us, I should prefer to postpone for the present any further treatment of this subject. Nevertheless, as all the experiments I have hitherto made tend, without exception, to substantiate my views, it will at least be interesting to describe those experiments in connexion with the theory which led to their being tried. The theory in question is a theory of ganglionic action in general.

I think every one will feel it to be obviously true that if ganglionic action is ever to receive any considerable elucidation, the Medusæ are by far the most promising structures to yield it. In them we have the first observed appearance, in the ascending scale of animal life, both of nervous and of muscular elements. These elements are, therefore, presumably here present in their simplest or most primitive forms. Again, the organisms are of all sizes, from less than that of a pea to more than that of a parasol ; their endurance under experimentation is as great as can be desired ; in their different species they present countless modifications of structure, and, in general, they present what one may regard as a typically perfect class of tissues for the purposes of

that special division of physiological inquiry to which I have referred. If, therefore, I have been able to detect any peculiarities in the functions of these primitive ganglionic tissues which have not hitherto been detected in the ganglionic tissues of higher animals, I cannot but consider it legitimate to attach a high degree of theoretical importance to such peculiarities; for I think it then becomes legitimate to feel that such peculiarities ground a strong analogy in favour of the belief, that whether or not similar functions admit of being experimentally proved in ganglionic tissues elsewhere, such functions are probably present wherever ganglionic action can be shown to occur, and that however hopelessly these functions may be obscured by the new and complex relations that in other cases are involved, they nevertheless constitute in every case some among the fundamental properties of ganglionic tissue.

Now, viewed in this manner, I think that the strictly rhythmic action of the paralyzed swimming-bell of *Aurelia* in answer to constant stimulation is a fact of the highest significance; for here we have a tissue wholly, or almost wholly, deprived of its centres of spontaneity, yet pulsating as rhythmically in answer to artificial stimulation as it previously did in answer to ganglionic stimulation.* Does not this tend to show that for the production of the natural rhythm the presence of the ganglionic element is non-essential; that if we merely suppose the function of this element to be that of supplying a constant stimulus of a low intensity without in addition supposing the presence of any special resistance mechanism to regulate the discharges, the periodic sequence of systole and diastole would assuredly result; and, therefore, that the *rhythmical* character of the natural swimming motions is dependent, not on the peculiar relations of the ganglionic, but on the primary qualities of the contractile tissue? Or, if we do not go so far as this (and, as I shall conclude by explaining, I am not myself inclined to go so far), must we not at least conclude that the natural rhythm of these tissues is not *exclusively* due to any mechanism whereby the discharges of the ganglia are interrupted at regular intervals; but that whether these discharges are supposed to be interrupted or continuous, the natural rhythm is probably in a large measure due to the same cause as the artificial rhythm—viz.: in accordance with our previous hypothesis, to the alternate exhaustion and recovery of the excitable tissues? This much, at least, must be allowed even by the most cautious of critics, viz.: that if, as current views respecting the theory of rhythm would suppose, it is exclusively the ganglionic element which in the unmutilated *Aurelia* causes the rhythm of the swimming-motions by intermittent stimulation, surely it becomes a most unexpected and unaccountable fact, that after the removal of this element the contractile tissues should still persist in their display of rhythm under the influence of constant stimulation. At any rate, no one, I think, will dispute that the

* It will not be forgotten that there are a multitude of ganglion-cells distributed throughout the contractile tissues of the Medusæ, but forasmuch as these are comparatively rarely instrumental in originating stimulation, I think it is probable that artificial stimulation acts directly on the contractile tissues, and not through the medium of these scattered cells.

facts which I have adduced justify us in reconsidering the whole theory of rhythm as due to ganglia.

(*k.*) As I have already said, I am not inclined to deny that there is probably some truth in the current theory of rhythm as due to ganglia; I merely wish to point out distinctly that this theory is inadequate, and that in order to cover all the facts, it will require to be supplemented by the theory which I now propose. The current theory of rhythm as due to ganglia attributes the whole of the effect to the ganglionic element, and thus fails to meet the facts of a rhythm which is artificially produced after the ganglionic element has been removed. It also fails to meet a number of other facts of the first importance. For it is beyond all doubt that rhythmic action of the strictest kind occurs in an innumerable multitude of cases where it is quite impossible to suppose anything resembling ganglia to be present. Not to mention such cases as the Snail's heart, where the most careful scrutiny has failed to detect the least vestige of ganglia, but to descend at once to the lowest forms of animal and vegetable life, rhythmic action may here be said to be the rule rather than the exception. The beautifully regular motions observable in some Algæ, Diatomaceæ, and Ocillatoriæ, in countless numbers of Infusoria, antherozoids, and spermatozoa, in ciliary action, and even in the petioles of *Hedysarum gyrans*, are all instances (to which many others might be added) of rhythmical action where the presence of ganglia is out of the question. Again, in a general way, is it not just as we recede from these primitive forms of contractile tissue that we find rhythmic action to become less usual? And, if this is so, may it not be that those contractile tissues which in the higher animals manifest rhythmic action are the contractile tissues which have longest retained their primitive endowment of rhythmicality? To my mind it seems hard to decide in what respect the beating of a Snail's heart differs from that of the pulsatile vesicles of the Infusoria; and I do not think it would be much easier to decide in what essential respect it differs from the beating of the Mammalian heart. The mere fact that the presence of ganglia can be proved in the one case and not in the other, seems to me scarcely to justify the conclusion that the rhythm is in the one case wholly dependent, and in the other as wholly independent, of the ganglia. At any rate, this fact, if it is a fact, is not of so self-evident a character as to recommend to us the current theory of ganglionic action on *à priori* grounds.

(*l.*) Coming, then, to experimental tests, we have already seen that in the deganglionated swimming organ of *Aurelia aurita*, rhythmic response is yielded to constant faradaic stimulation of low intensity. The next question, therefore, which presents itself in relation to our subject, is as to whether other modes of constant stimulation elicit a similar response. Now, in a general way, I may say that such is the case, although I have chosen faradaic stimulation for special mention, because, in the first place, its effect in producing rhythmic action is the most certain and precise, and, in the next place, the effects of administering instantaneous shocks at given intervals admit of being compared with the effects of constant faradaic stimulation

better than with any other kind of constant stimulation. Nevertheless, as just stated, other modes of constant stimulation certainly have a more or less marked effect in producing rhythmic response. As mentioned incidentally in my first paper, the constant current, during the whole time of its passage, frequently has this effect in the case of the paralyzed nectocalyx of *Sarsia* (p. 282). At the time I published that paper I had not observed the rhythm due to faradaic stimulation, and so suggested that the response in this case was "perhaps due to the hydrogen bubbles acting as stimulants to contraction." Now, however, I am inclined to think, from the analogy supplied by the effects of the faradaic current, that the rhythmic response to the constant current is not due to any such accidental cause.

With regard to other modes of stimulation, I may in the first instance refer to Division III., §§ 1 and 2, of my second paper. It is there stated: " When the paralyzed swimming organ of *Aurelia aurita* is stimulated by a single mechanical irritation, it often responds with two, and more rarely with three contractions, which are separated from one another by an interval of about the same length as the normal diastole of the unmutilated animal. . . . . Dilute spirit, or other irritant, when dropped on the paralyzed swimming organ of *Aurelia aurita*, often gives rise to a whole series of rhythmical pulsations, the systoles and diastoles following one another at about the same rate as is observable in the normal swimming motions of the unmutilated animal."

From this it will be seen that both in the case of mechanical and of chemical stimulation the same tendency to the production of rhythmic response on the part of the paralyzed tissues of *Aurelia* may be observed, as in the case of electrical stimulation. The principal differences consist in the rhythm being much less sustained in the former than in the latter case. But by experimenting on other species of Medusæ I have been able to obtain artificial rhythm in response to mechanical and chemical stimulation of a much more sustained character than that which, under such modes of stimulation, occurs in *Aurelia*. I have no explanation to offer why it is that some species or some tissues present so much more readiness to manifest sustained rhythm under certain modes of stimulation, and less readiness to manifest it under other modes, than do other species or tissues. Probably these differences depend on some peculiarities in the irritability of the tissues which it is hopeless to ascertain ; but, in any case, the fact remains that while *Aurelia*, *Cyanœa*, and the covered-eyed Medusæ generally, are the best species for obtaining artificial rhythm under the influence of faradaic stimulation, some of the naked-eyed Medusæ are the best species for obtaining it under the influence of the constant current, and also under that of mechanical and chemical stimulation. I have already spoken of this effect of the constant current in the case of *Sarsia ;* I shall now proceed to describe the effects of mechanical and chemical stimulation on the same species.

It is but rarely that artificial rhythm can be produced in the paralyzed nectocalyx of *Sarsia* by means of mechanical stimulation, but in the case of the polypite, a very decided, peculiar, and persistent rhythm admits of being produced by this means.

In this particular species the polypite never exhibits any spontaneous motion after the ganglia of the nectocalyx have been removed. But if it be nipped with the forceps, or otherwise irritated, it contracts strongly and suddenly; it then very slowly and gradually relaxes until it has regained its original length. After a considerable interval, and without the application of any additional stimulus, it gives another single, sudden, though slight contraction, to be again followed by gradual relaxation and a prolonged interval of repose, which is followed in turn by another contraction, and so on. These sudden and well-marked contractions occur at intervals of many seconds, and show a decided tendency to rhythmic periodicity, though the rhythm is not always perfectly exact. This intensely slow rhythm as the result of injury may continue for a long time, particularly if the injury has been of a severe character. There can be no doubt, therefore, that the mechanical (or other) injury in this case acts as a source of constant irritation; so that here again we have evidence of rhythmic action independent of ganglia and caused by the alternate exhaustion and recovery of contractile tissues.*

With regard to artificial rhythm caused by chemical stimuli, by far the most conspicuous instance that I have observed is that of the paralyzed nectocalyx of *Sarsia*. It will be remembered that in my first paper, under the heading " STIMULATION," I drew prominent attention to " a highly peculiar motion of a flurried, shivering character," which is manifested by this organ when its marginal ganglia have been removed and it is exposed to the influence of faintly acidulated water. As previously remarked, at the time when this description was published I had not observed the phenomena of artificial rhythm in any of the other cases in which I subsequently observed it, and I was therefore completely at a loss to interpret the facts in the case which I described. I was thus under the necessity of stating the fact merely as " a highly remarkable phenomenon, and one which I was quite unable to explain, though I was persuaded that it was a phenomenon well meriting the attention of physiologists." Now, however, when read in the light of the foregoing facts, there can be no doubt that the present one falls into its place very satisfactorily; it is an additional and very valuable instance of the display of artificial rhythm under the influence of a constant stimulus of low intensity. For the shivering motions of

* We may pretty safely conclude that ganglia are altogether absent in the polypite of *Sarsia*, not only because SCHULTZ has failed to detect them in this organ microscopically, but also because of the complete absence of spontaneity which it manifests. I may here mention that this case of the polypite of *Sarsia* is precisely analagous to another which I have observed in a widely different tissue, namely, the tongue of the Frog. Here, too, the presence of ganglion cells has never been observed microscopically, though specially sought for by Dr. KLEIN and others. Yet under the influence of mechanical and other modes of stimulation, I find that I am able to make the excised organ pulsate as rhythmically as a heart. As however I intend to devote a separate paper to the subject of artificial rhythm in tissues other than those of the Medusæ, I shall not here enter into details with regard to the singularly beautiful instance which I have just mentioned; but I have felt that it is desirable to point out in this place the analogy which it presents to the case of the polypite of *Sarsia*.

the mutilated nectocalyx under these circumstances are most unmistakably of a rhythmic nature. Viewed from a little distance, indeed, these motions are not distinguishable from the natural swimming motions of the unmutilated animal, except that, not being of quite such a powerful character, they are not so effective for locomotion. Viewed more closely, however, it may frequently be seen that the whole bell does not contract simultaneously, but that, as it were, clouds of contraction pass now over one part and now over another. Still, whether the contractions are partial or universal, they are always more or less rhythmical. As this is the only case that has ever been observed of rhythm as due to a constant chemical stimulus, I have studied it with much care, and shall now give a full description of what appears to me an important body of physiological facts.

Ten to twenty drops of acetic acid having been added to 1000 c.c. of sea-water, and the paralyzed bell of *Sarsia* having been placed in the mixture, an interval of about half a minute will elapse before any movement begins. Sooner or later, however, the artificial rhythm is sure to be induced, and it will then continue for a variable time—occasionally as long as an hour, and generally for a considerable number of minutes. After it ceases it may often be made to recommence, either by adding a few more drops of acid to the sea-water, or by supplying an additional stimulus to the bell by nipping it with the forceps. Eventually, however, all movement ceases, owing to the destruction of irritability by the action of the acid. By this time the whole inner surface of the bell has become strongly opalescent, owing to the destructive influence of the acid on the epithelial cells which overspread the irritable tissues. The latter fact is worth mentioning, because in no case does the artificial rhythm set in until this opalescence has begun to show itself; and as this opalescence is but an optical expression of the damage which the epithelial coat is undergoing, the explanation of the time which elapses after the first immersion of the bell in the acidulated water and the commencement of the artificial rhythm, no doubt is that during this time the acid has not obtained sufficient access to the excitable tissues to serve as an adequate stimulus.

During the soaking stage of the experiment—*i.e.*, before the artificial rhythm begins—the excitability of the tissues may be observed progressively and abnormally to increase; for soon after the soaking stage begins, in response to a single nip with the forceps the bell may give two or three locomotor contractions, instead of a single one, as is *invariably* the case with a paralyzed bell of *Sarsia* in normal water. Later on during the soaking stage four or five successive contractions may be yielded in response to a single mechanical stimulus, and shortly after this a whole bout of rhythmic contractions may be started by the same means. Indeed, in some cases the artificial rhythm in acidulated water requires such a single additional stimulus for its inauguration—the shivering movement failing to begin spontaneously, but beginning immediately upon the application of the additional stimulus. Similarly, after the shivering movements have ceased, a fresh bout may very often be started by again giving the

motionless nectocalyx a single stimulation. The interpretation of these facts would seem to be that the general irritability of the excitable tissues is exalted by the universal and constant stimulus supplied by the acid to an extent that is just bordering on that which gives rise to rhythmic movement, so that when the violent contraction is given in response to the mechanical stimulus, the disturbance serves to start the rhythmic movement.

If a paralyzed nectocalyx, while manifesting its artificial rhythm in acidulated sea-water, be suddenly transferred to normal sea-water, the movements do not cease immediately, but continue for a considerable time. This fact can easily be explained by the very probable, and indeed almost necessary, supposition that it takes some time after the transference to the normal sea-water for the acid to be washed out from contact with the excitable tissues. Sooner or later, however, as we should expect, in the normal sea-water the rhythmic movements entirely cease, and the bell becomes quiescent, with a normal irritability as regards single stimuli. If it be now again transferred to the acidulated water, after a short interval the rhythmic movements will again commence—and so on during several repetitions of this experiment, until the irritability of the tissues has finally become destroyed by the influence of the acid.

Other chemical irritants which I have tried produce substantially similar effects on the paralyzed bells of *Sarsia*. I shall therefore only wait to describe the influence of one of these irritants, the action of which in some respects differs from that of acids, and which I have found to be one of the most unfailing in its power to produce the rhythmic movements in question. This irritant is glycerine, and in order to produce its full effect it requires to be added to the sea-water in about the proportion of 5 per cent. The manifestation of artificial rhythm in solutions of this kind is quite unfailing. It begins after an exposure of from 15 to 30 seconds, and continues for a variable number of seconds. It generally begins with powerful contractions, of a less shivering character than those which are produced by acids, and therefore still more closely resembling the normal swimming motions of the unmutilated animal. Sometimes, however, the first manifestation of the artificial rhythm is in the form of a few gentle rhythmic contractions, to be followed by a few seconds of quiescence, and then by the commencement of the sustained bout of strong contractions. In either case, when the bout of strong contractions sets in, the rate of the rhythm becomes progressively and rapidly increased, until in a few seconds it runs up into incipient tetanus. The rate of the rhythm still quickening, the tetanus rapidly becomes more and more pronounced, till at last the bell becomes quiescent in tonic spasm.*

If the bell is still left in the glycerine solution nothing further happens ; the tissues

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* Sometimes, however, the order of events is slightly different, the advent of the spasm being more sudden, and followed by a mitigation of its severity, the bell then exhibiting what is more usually the first phase of the series—namely, the occurrence of the locomotor-like contractions. Occasionally, also, rhythmical shivering contractions may be seen superimposed on the general tonic contraction, either in a part or over the whole of the contractile tissues.

die in this condition of strong systole. But if the bell be transferred to normal sea-water immediately after, or still better, slightly before the tonic spasm has become complete, an interesting series of phenomena present themselves. The spasm persists for a long time after the transference without undergoing any change—the length of this time depending on the stage in the severity of the spasm at which the transference is made. After this time is passed, the spasm becomes less pronounced than it was at the moment of transference, and a reversion takes place to the rhythmic contractions. The spasm may next pass off entirely, leaving only the rhythmic contractions behind. Eventually these too fade away into quiescence; but it is remarkable that they leave behind them a much more persistent exaltation of irritability than is the case with acid. For in the case of glycerine the paralyzed bell which has been exposed to the influence of the irritant and afterwards become quiescent in normal sea-water, will often continue for hours to respond to single stimuli with a bout of rhythmic contractions. This effect of glycerine in producing an extreme condition of exalted irritability is also rendered apparent in another way. For if, during the soaking stage of the experiment—i.e., before the first of the rhythmic contractions has occurred—the bell be nipped with the forceps, the effect may be that of so precipitating events that the whole of the rhythmic stages are omitted, and the previously quiescent bell enters at once into a state of rigid tonic spasm. This effect is particularly liable to occur after prolonged soaking in weak solutions of glycerine.

As in the case of stimulation by acid, so in that of stimulation by glycerine, the artificial rhythm never begins in any strength of solution until the epithelial surface has become opalescent to a considerable degree.

In the case of stimulation by glycerine the behaviour of the polypite is more unequivocal than it is in the case of stimulation by acid. I have therefore reserved till now my description of the behaviour of this organ under the influence of constant chemical stimulation. This behaviour is of a very marked though simple character. The polypite is always the first to respond to the stimulation—its retraction preceding the first movements of the bell by an interval of several seconds, so that by the time the bell begins its rhythmic response the polypite is usually retracted to its utmost. The initial response of the polypite is also rhythmic; and the rhythm which it manifests—especially if the glycerine solution be not over strong—is of the same slow character which has already been described as manifested by this organ when under the influence of mechanical stimulation. The rhythm, however, is decidedly quicker in the former than in the latter case.

Lastly, with regard to the marginal ganglia, it is to be observed that in the case of all the chemical irritants I have tried, if unmutilated specimens of Sarsia be immersed in a sea-water solution of the irritant, which is of a sufficient strength to evoke artificial rhythm in paralyzed specimens, the spontaneity of the ganglia is destroyed in a few seconds after the immersion of the animals—i.e., in a shorter time than is required for the first appearance of artificial rhythm. Consequently, whether the

specimens experimented upon be entire or paralyzed by removal of their margins, the phenomena of artificial rhythm under the influence of chemical stimulation are the same. But although the spontaneity of the ganglia disappears before the artificial rhythm sets in, such is not the case with the reflex activity of the ganglia; for on nipping a tentacle of the quiescent bell before the artificial rhythm has set in, the bell will give a single normal response to the stimulation.

Hence, in historical order, on dropping an unmutilated specimen into a solution of glycerine of the strength named, the usual succession of events to be observed is as follows :—First, increased activity of the normal swimming-motions, to be quickly followed by a rapid and progressive decrease of such activity, till in about fifteen seconds after the immersion total quiescence supervenes. Four or five seconds later the polypite begins to retract by rhythmical twitches, the rate of this rhythm rapidly increasing until it ends in tonic contraction. When the polypite has just become fully retracted—or very often a little earlier—the bell suddenly begins its forcible and well-pronounced rhythmic contractions, which rapidly increase in their rate of rhythm, until they coalesce into a vigorous and persistent spasm. If the animal be now restored to normal sea-water, spontaneity will return in a feeble manner; but there is always afterwards a great tendency displayed by the bell to exhibit shivering spasms instead of normal swimming movements in response to natural or ganglionic stimulation. And, as already observed, this peculiarity of the excitable tissues is also well marked in the case of the artificial stimulation of deganglionated specimens under otherwise similar circumstances.

The only facts which still remain to be considered regarding these shivering movements of paralyzed *Sarsia* are those which have reference to electrical stimulation. It will be remembered that in my first paper (*loc. cit.*) I described these shivering movements as ensuing, not only when the paralyzed bells are immersed in chemical stimulants, but also when they are immersed in normal sea-water immediately after having been submitted to electrical stimulation. As the passage in my former paper which describes this effect of electrical stimulation is a short one, I will here transcribe it:—

" When the swimming-bell of *Sarsia* has had its margin removed, and so, as proved by hundreds of similar experiments, has been entirely deprived of its locomotor centres, nevertheless, in response to electrical stimulation, instead of giving a single contraction to make or break, it may begin a highly peculiar motion of a flurried, shivering character, which lasts without intermission for periods varying from a few seconds to half an hour. I never but once saw a similar motion in the perfect animal, and this was in the case of a specimen which was dying from having been poisoned with iron rust. The motion, I think, can be explained by supposing that the various parts of the muscle-layer are contracting without co-ordination; but why they should sometimes do this in response to stimulation, and why when they do this they should continue the action so long, these questions I cannot answer. In the case of so peculiar a

phenomenon, however, it is necessary that I should detail all the facts I have been able to collect. I have never seen any similar or corresponding action performed by the bells of other medusids, and even in the case of *Sarsia* its occurrence is comparatively rare. When it does occur, however, it is always continuous ; that is to say, it never spontaneously recommences after having once ceased. As already stated, the period of its duration is extremely variable ; but when this period is long, it is observable that the shivering motions become feebler and feebler, until they eventually fade away into quiescence. The animal is then quite dead to all further stimulation. Beyond saying that the peculiar motions in question never originate independently of stimulation, I cannot give much further account of the conditions which determine their commencement. The following instances are quoted from my notes *in extenso :*

' A healthy individual with centres removed, after failing to respond to either make or break of direct current, and after about a quarter of a minute's rest from a series of rapidly alternating makes and breaks of this current, began to shiver, and continued to do so for five minutes. Afterwards quite dead.'

" ' Another healthy individual, after refusing to contract either on make or break of induced current for two or three times, began to shiver, and continued to do so for twenty minutes. Afterwards quite dead. This individual had been used five minutes before for experiments with the direct current, to which it responded well and without shivering.'

" ' Another healthy individual was left for some time after excision of margin, and then put into the well and submitted to induction-shocks. No contraction either on make or break with coil pushed to zero. On now trying direct current, without altering position of electrodes, violent contraction on make and also a decided one on break. On again trying induced current, no contraction. On again trying direct current, strong contractions [thus far, of course, the behavior of the tissue was normal, see above § 2 (A)], and after four or five of these, shivering began ; this lasted for four minutes, and, when again quiescent, the bell again responded to make and break of direct current in the ordinary way.'

" Now all that can be gathered from these and similar notes is, that the shivering motion in question may be started either by the direct or by the induced current, and this in some cases when the bell has repeatedly refused to answer stimuli in the ordinary way. It may further be gathered from these notes that shivering is most likely to begin after the bell has received a number of shocks in succession."

The passage concludes by observing that the shivering movements in question are much more certain to be produced by means of chemical stimulation, as just described in the previous paragraphs of the present paper. Now, when we consider these results of electrical stimulation in the light which has since been shed by the results of all the other experiments on artificial rhythm, there can be no doubt that in some way or other the injury which the electrical stimulation has previously supplied to the tissue continues for a long time afterwards to act as a constant stimulus to these

tissues, and thus occasionally throws them into artificial rhythm. What the precise nature of this injury may be is a matter of subordinate interest; but I may state that I have never observed artificial rhythm to occur as a result of electrical stimulation until the latter has acted for a sufficient length of time to cause an opalescence of the tissues in the neighbourhood of the electrodes. This opalescence, in the case of *Sarsia*, is always certain to manifest itself under the influence of an electrical stimulus of sufficient duration, and when it does manifest itself it is indistinguishable from that which has already been described as the result of chemical action. There can then be no doubt that artificial rhythm as an after-effect of electrical stimulation never asserts itself until after that stimulation has inflicted a conspicuous injury upon the tissues. But in order to assure myself still more effectually that the artificial rhythm in this case is due to a constant stimulus supplied by a local injury in the region where the electrodes had rested, I tried the following experiment. Having submitted a paralyzed bell of *Sarsia* to a number of successive electrical shocks in the same area of its excitable surface, and having then observed, on removing the electrodes and allowing the mutilated bell to float freely in the water, that the artificial rhythm was in vigorous progress, I suddenly with two snips of the scissors excised the area of tissue which had previously been the seat of electrical stimulation. Instantly all movement ceased. This experiment, therefore, proved that the rhythmic movements can only have been due to a stimulus emanating from the seat of injury, and continuously spreading over all the other parts of the excitable surface of the bell. And, such being the case, we can have no further doubt that the case of artificial rhythm due to previous electrical stimulation belongs to the same category of physiological facts as the case of artificial rhythm due to present or previous chemical stimulation. For now, in conclusion, I may observe that in order to render the experimental parallel complete, I imitated in the case of chemical stimulation the proof of the fact which I have just narrated in the case of electrical stimulation, viz.: that the artificial rhythm depends on the continuous reception by the excitable tissues of a stimulus which is continuously supplied from a seat, or seats, of injury. The method which I employed to prove this fact in the case of chemical stimulation was as follows. Having slit open the paralyzed bell of *Sarsia* along the whole of one side from base to apex of the cone, I suspended the now sheet-like mass of tissue by one corner in the air, leaving the rest of the sheet to hang vertically downwards. By means of a rack-work support I now lowered the sheet of tissue till one portion of it dipped into a beaker filled with a solution of glycerine of appropriate strength. After allowing this portion to soak in the solution of glycerine until it became slightly opalescent, I dropped the entire mutilated bell, or sheet of tissue, into another beaker containing ordinary sea-water. If the exposure to the glycerine solution had been of sufficient duration, I invariably found that in the normal sea-water the rhythmic movements were performed by the whole tissue mass quite as efficiently as was the case in my other experiments, where the whole tissue-mass, and not merely a portion, had been submitted to the influence of the irritant. But on now

suddenly snipping off the opalescent portion of the tissue-mass—*i.e.*, the portion which had been previously alone submitted to the influence of the irritant—all movement in the remainder of the tissue-mass instantly ceased. This experiment I performed repeatedly, sometimes exposing a large and sometimes a small portion of the tissue to the influence of the irritant. As I invariably obtained the same result, there can be no doubt that in the case of chemical, as in that of the after-effects of electrical stimulation, the artificial rhythm depends for its manifestation on the presence of a constant stimulus, and is not merely some kind of obscure fluttering motion which, having been started by a stimulus, is afterwards kept up independently of any stimulus.

Such being the case, I naturally expected that if I were to supply a constant stimulus of a thermal kind I should also obtain the phenomena of artificial rhythm. In this, however, my expectations have not been realised. With no species of Medusa have I been able to obtain the slightest indication of artificial rhythm by immersing the paralyzed animals in heated water. I can only explain this fact by supposing that the stimulus which is supplied by the heated medium is of too uniform a character over the whole extent of the excitable tissues; it would seem that in order to produce artificial rhythm there must be a differential intensity of stimulation in different parts of the responding tissue, for no doubt even the excitatory influence of acidulated water is not of nearly so uniform an intensity over the whole of the tissue area as is that of heated water.

In now quitting the subject of artificial rhythm as it is manifested by the paralyzed bells of *Sarsia*, it is desirable again to observe that sustained artificial rhythm cannot be produced either by means of chemical irritation or as the after-effect of electrical stimulation in the case of any of the species of covered-eyed Medusæ that I have met with. In order to evoke any response at all, stronger solutions of the irritants require to be employed in the case of the covered- than in that of the naked-eyed Medusæ, and when the responses do occur they are not of so suggestive a character as those which I have thought it worth while so fully to describe. Nevertheless, even in the covered-eyed Medusæ well marked, though comparatively brief, displays of artificial rhythm may often be observed as the result of constant chemical stimulation. Thus, for instance, in the case of *Aurelia*, if the paralyzed umbrella be immersed in a solution of glycerine (10 to 20 per cent.) a few rhythmic pulsations of normal rate are usually given, but shortly after these pulsations occur the tissue begins to go into a tetanus, which progressively and rapidly becomes more and more pronounced until it ends in violent tonic spasm. So that the history of events really resembles that of *Sarsia* under similar circumstances, except that the stage of artificial rhythm which inaugurates the spasm is of a character comparatively less pronounced.

(*m.*) Thus far, then, I have detailed all the facts which I have been able to collect with reference to the phenomena of artificial rhythm as produced by different kinds of constant stimulation. It will not be forgotten that the interest attaching to these facts arises from the bearing which they have on the theory of natural rhythm. My

belief is that hitherto the theory of rhythm as due to ganglia has attributed far too much importance to the ganglionic as distinguished from the contractile tissues, and I have founded this belief principally on the facts which have been already stated and which certainly prove, at least, this much : that after the removal of their centres of spontaneity the contractile tissues of the Medusæ display a marked and persistent tendency to break into rhythmic action whenever they are supplied with a constant stimulus of feeble intensity. Without waiting again to indicate how this fact tends to suggest that the natural rhythm of the unmutilated organisms is probably in large part due to that alternate process of exhaustion and restoration of excitability on the part of the contractile tissues, whereby alone the phenomena of artificial rhythm can be explained,* I shall go on to describe some further experiments which were designed to test the question whether the influences which affect the character of the natural rhythm likewise, and in the same manner, affect the character of the artificial rhythm. I took the trouble to perform these experiments because I felt that if they should result in answering this question in the affirmative, they would tend still further to substantiate the view I am endeavouring to uphold, viz.: that the natural rhythm may be a function of the contractile as distinguished from the ganglionic tissue. Of the modifying causes in question, the first that I tried was temperature.

(n.) Having already, in my former paper, treated of the effects of temperature on the natural rhythm, it will now be sufficient to say that we have seen these effects to be similar to those which temperature exerts on the rhythm of ganglionic tissues in general. Now I find that temperature exerts precisely the same influence on the artificial rhythm of deganglionated tissue as it does on the natural rhythm of the unmutilated animal. To economise space I shall only quote one of my observations in a table which explains itself. I also append tracings of another observation to render the difference in the rate of the rhythm more apparent to the eye.†

Temperature of water (Fahr.).	Number of contractions per minute.
25°	24
45°	40
75°	60

* It is of importance to point out the fact that some of my previously published experiments appear conclusively to prove that the natural stimulation which is supplied by the marginal ganglia of the Medusæ resembles all the modes of artificial stimulation which are competent to produce artificial rhythm in one important particular; the *intensity* of the stimulation which the marginal ganglia supply is shown by these experiments to be about the same as that which is required to produce artificial rhythm in the case of artificial stimulation. In proof of this point I may allude particularly to the observations which are detailed in V., § 1 (a), (b), and (c) of my second paper.

† As the effects of temperature in modifying the rate of artificial rhythm no doubt arise from the effects of temperature on modifying the excitability of the contractile tissues, I think it is desirable here again to mention a fact which was briefly stated in my second paper (p. 691), viz.: that in the excitable tissues of the Medusæ, temperature exerts an immense influence, both on the latent period and on the activity
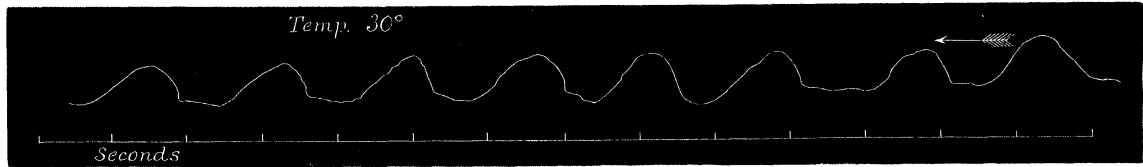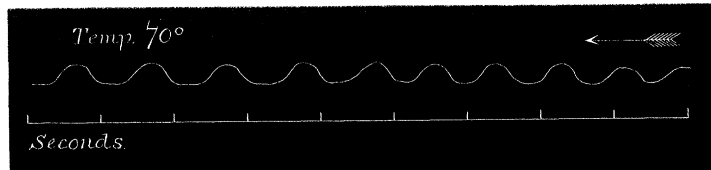
Fig. 5.

Fig. 6.

During the whole progress of such experiments the faradaic stimulation was, of course, kept of uniform intensity; so that the progressive acceleration is undoubtedly due to the increase of temperature alone. With each increment of temperature the rate of the artificial rhythm increases suddenly, just as it does in the case of the natural rhythm. Moreover, there seems to be a sort of rough correspondence between the amount of influence that any given degree of temperature exerts on the rate of the natural and of the artificial rhythm respectively; for it will be remembered that in warm water the natural rhythm, besides being quicker, is not so regular as it is in cold water; thus also it is with the artificial rhythm. Again, water below 20° or above 85° suspends the natural rhythm, i.e., stops the contractions; and the artificial rhythm is suspended at about the same degrees. Lastly, just as there are considerable individual variations in the extent to which the natural rhythm is affected by temperature, so the artificial rhythm is in some cases more affected by this cause than in others, though in all cases it further resembles the natural rhythm in showing some considerable degree of modification under the influence of this cause.

On the whole, then, it would be impossible to imagine two cases more completely parallel than are these of the effects of temperature on natural and on artificial rhythm

of contraction. To render apparent the degree in which these effects are produced, I here append a pair of tracings which were procured from the same piece of tissue when exposed to the different temperatures named. (N.B.—The seconds are wrongly marked in fig. 8, they ought to be the same as in fig. 7.)
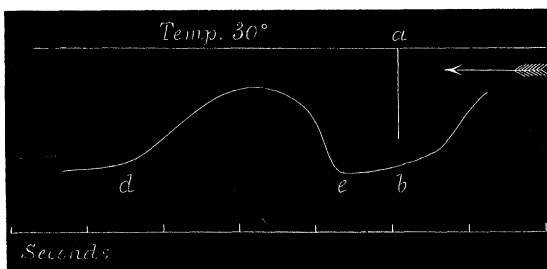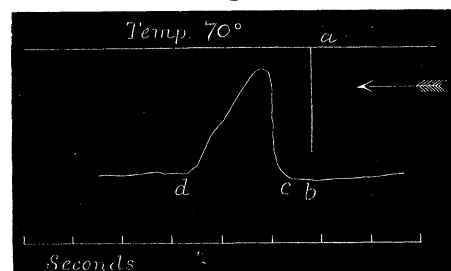
Fig. 7.   Fig. 8.

respectively; and as it must be considered in the last degree improbable that all these coincidences are accidental, I conclude that the effects of temperature on the natural rhythm of Medusæ (and so, in all probability, on the natural rhythm of other ganglio-muscular tissues) are for the most part exerted, not on the ganglionic, but on the contractile element.

(*o.*) In order to test the effects of gases on the artificial rhythm, I took a severed quadrant of *Aurelia*, and floated it in sea-water with its muscular surface just above the level of the water. Over the tissue I lowered an inverted beaker filled with the gas, the effects of which I desired to ascertain, and by progressively forcing the rim of the beaker into the water I could submit the tissue to various pressures of the atmosphere of the gas I was using. By an appropriate arrangement the electrodes passed into the interior of the beaker, and could then be manipulated from the outside, so as to be properly adjusted on the tissue. In this way I was able to observe that different gases exerted a marked influence on the rate of the artificial rhythm. My experiments, however, in this connexion are not as yet complete; so I shall now confine myself to saying that an atmosphere of oxygen appears to accelerate the artificial rhythm, while an atmosphere of carbonic acid certainly retards it—the rate of the rhythm in air being in both cases taken as the standard of comparison, and the intensity of the faradaic stimulation remaining constant throughout the three observations. The following table gives the ratios in the case of one experiment :—

Rate of artificial rhythm, in air.	In oxygen.	In carbonic acid.
36 per minute.	50 per minute.	25 per minute.

It may here be observed that, to produce these results, both carbonic acid and oxygen must be considerably diluted with air; for otherwise they have the effect of instantaneously inhibiting all response, even to the strongest stimulation. When this is the case, however, irritability returns very soon after the tissue is again exposed to air or to ordinary sea-water. But I desire it to be distinctly understood that the results of my experiments on the influence of oxygen, both on the natural and on the artificial rhythm, have proved singularly equivocal; so that as far as this gas is concerned further observations are required before the above results can be accepted as certain.

(*p.*) I have still one other observation of a very interesting character to describe, which is closely connected with the current views respecting ganglionic action, and may therefore be more conveniently considered here than in any other part of this paper. In my first paper I stated that in no case had I observed the manubrium, or polypite, of a Medusa to be affected, " as to its natural motions," by removal of the periphery of the swimming-bell. This statement still remains true; but in the case of *Sarsia* a very interesting change occurs in the polypite soon after the nectocalyx has been paralyzed by excision of its margin. Unlike the polypites of most of the other

Medusæ, this organ, in the case of *Sarsia*, is very highly retractile. In fresh and lively specimens the appendage in question is carried in its retracted state ; but when the animals become less vigorous—from the warmth or impurity of the water in which they are confined, or from any other cause—their polypites usually become relaxed. The relaxation may show itself in various degrees in different specimens subjected to the same conditions ; but in no case is the degree of relaxation so remarkable as that which may be caused by removing the periphery of the nectocalyx. For the purpose of showing this effect, it does not signify in what condition as to vigour, &c., the specimen chosen happens to be in ; for whether the polypite prior to the operation be contracted or partially relaxed, within half an hour after the operation it is sure to become lengthened to a considerable extent.

In order to show the surprising degree to which this extention may proceed, I insert a sketch of a specimen both before and after the operation. The sketches are of life size, and drawn to accurate measurement (figs. 9 and 10).*

Fig. 9.

Fig. 10.

With regard to this remarkable effect on the polypite of removing the margin of the nectocalyx, it is now to be observed that in it we appear to have very unexceptionable evidence of such a relation subsisting between the ganglia of the nectocalyx and the muscular fibres of the polypite, as elsewhere gives rise to what is known as muscular tonus. This interpretation of the facts cannot, I think, be disputed ; and it fully explains why, in the unmutilated animal, the degree of elongation on the part of the polypite usually exhibits an inverse proportion to the degree of locomotor activity displayed by the bell. I may here state that I have also observed indications of muscular tonus in some of the other Medusæ, but for the sake of brevity I shall here restrict myself to the consideration of this one case.

* I may here mention that the fact of the polypite of *Sarsia* undergoing this extreme elongation after the removal of the marginal ganglia, serves to render the artificial rhythm of the organ under the influence of injury, as previously described, all the more conspicuous.

To my mind, then, it is an interesting fact that ganglionic tissue, where it can first be shown to occur in the animal kingdom, has for one of its functions the maintenance of muscular tonus; but it is not on this account that I now wish to draw prominent attention to the fact before us.   Physiologists are almost unanimous in regarding muscular tonus as a kind of gentle tetanus due to a persistent ganglionic stimulation ; and against this opinion it seems impossible to urge any valid objection.   But, in accordance with the accepted theory of ganglionic action, physiologists further suppose that the only reason why some muscles are thrown into a state of tonus by gang-lionic stimulation, while other muscles are thrown into a state of rhythmic action by the same means, is because the resistance to the passage of the stimulation from the ganglion to the muscle is less in the former than in the latter case.   Here, be it remembered, we are in the domain of pure speculation ; there is no experimental evidence to show that such a state of differential resistance as the theory requires really obtains.   Hence we are quite at liberty to suppose any other kind of difference to obtain, either to the exclusion of this one or in company with it.   Such a supposition I now wish to suggest, and it is this : That all rhythmical action being regarded as due (at any rate in large part) to the alternate exhaustion and restoration of excitability on the part of contractile tissues, the reason why continuous ganglionic stimulation produces incipient tetanus in the case of some muscles and rhythmic action in the case of others, is either wholly or partly because the irritability of the muscles in relation to the intensity of the stimulation is greater in the former than in the latter case.   If this supposition as to differential irritability be granted, my experiments on *Aurelia* prove that tetanus would result in the one case and rhythmic action in the other ; for it will be remembered that in these experiments, if the continuous faradaic stimulation were of somewhat more than minimal intensity, tetanus was the result, while if such stimulation were but of minimal intensity, the result was rhythmic action.   Now, that in the particular case of *Sarsia* the irritability of the tonically contracting polypite is higher than that of the rhythmically contracting bell is a matter, not of supposition, but of observable fact ; for not only is the polypite more irritable than the bell in response to direct stimulation of its own substance, but it is generally more so even when the stimuli are applied anywhere over the excitable tissues of the bell.   And from this it is evident that the phenomena of muscular tonus, as they occur in *Sarsia*, tend more in favour of the exhaustion than of the resistance theory.*

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* The evidence, however, is not altogether exclusive of the resistance theory, for it is quite possible that in addition to the high irritability of the polypite there may be conductile lines of low resistance connecting this organ with the marginal ganglia.   I entertain this supposition because, as afterwards explained in the text, I see reason to believe that the natural swimming movements of *Sarsia* are probably in part due to an intermittent discharge of the ganglia.   I think, therefore, that in this particular case the ganglia supply a tolerably constant stimulation to the polypite, while it is only at intervals that their energy overflows into the bell, and that the higher degree of irritability on the part of the polypite ensures the tonic response

(*q.*) I will now sum up this rather lengthy discussion.   The two theories of ganglionic action may be stated antithetically thus : In both theories the accumulation of energy by ganglia is supposed to be a continuous process ; but while the resistance theory supposes the rhythm to be exclusively due to an intermittent and periodic discharge of this accumulated energy on the part of the ganglionic tissues, the exhaustion theory supposes that the rhythm is largely due to a periodic process of exhaustion and recovery on the part of the responding tissues.   Now, I submit that my experiments have proved the former of these two theories inadequate to explain all the phenomena of rhythm as it occurs in the Medusæ.   For these experiments have shown that even after the removal of the only ganglia which serve as centres of natural stimulation, the excitable tissues still continue to manifest a very perfect rhythm under the influence of any mode of artificial stimulation (except heat), which is of a constant character and of an intensity sufficiently low not to produce tetanus.   And as I have proved that the rhythm thus artificially produced is almost certainly due to the alternate process of exhaustion and recovery which I have explained, there can scarcely be any doubt that in the natural rhythm this process plays an important part, particularly as we find that temperature and gases exert the same influences on the one rhythm as they do on the other.   And, as an additional reason for recognising the part which the contractile tissues probably play in the production of rhythm, I have pointed to the fact that in the great majority of cases in which rhythmic action occurs, the presence of ganglia cannot be suspected.   For it is among the lower forms of life, where ganglia are certainly absent, and where the functions of stimulation and contraction appear to be blended and diffused, that rhythmic action is of the most frequent occurrence ; and it is obvious with how much greater difficulty the resistance theory is here beset than is the one which I now propose.   Granted a diffused power of stimulation with a diffused power of response, and I see no essential difference between the rhythmic motions of the simplest organism and those of a deganglionated Medusa in acidulated water.

But now, in conclusion, I wish it to be distinctly understood that I am not attempting to overturn, but merely to supplement, the current theory of ganglionic action. My belief is that this theory is to a large extent a true one, but that in order to become a complete theory it must incorporate the facts and inferences which have now been fully detailed.   By a complete theory I mean, of course, a theory which will cover all the facts ; and forasmuch as the facts on which my inferences are founded

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of this organ at a small cost of nervous energy.   How far the rhythm of the nectocalyx is to be attributed to the resistance mechanism of the ganglia, and how far to the alternate exhaustion and recovery of the contractile tissues, I think it is impossible to determine, seeing that it is impossible exactly to imitate the natural ganglionic stimulation by artificial means.   But it is, I think, of importance to have ascertained at least this much : that in *Sarsia* the tonus of one organ and the rhythm of another, which apparently both received their stimulation from the same ganglia, must at any rate in part be attributed to a differential irritability of these organs as distinguished from their differential stimulation.

are to a large extent novel, I have thought it desirable to insist on their theoretical importance rather than on that of facts which are better known, and which serve to uphold existing views respecting the action of ganglia. Nevertheless, even within the limits of the Medusæ, I have found only too much reason for concluding that the full explanation of natural rhythm must be more complex than that which I believe to apply to artificial rhythm. In particular I may allude to the case of *Sarsia*. The artificial rhythm which may be produced in the paralyzed nectocalyx of this organism by means of a constant stimulation is of a widely different character from that which occurs in the unmutilated and healthy animal. The comparatively feeble, fluttering, and ineffectual sequence of contraction and relaxation in the former case contrast strongly with the powerful, determined, and pumping-like movement in the latter case. Indeed, striking and suggestive as are the phenomena of artificial rhythm in *Sarsia*, none but the most prejudiced of observers could fail to perceive that it is but a sorry substitute for the natural rhythm of vigorous specimens. In feeble specimens, no doubt, the natural rhythm resembles much more closely the artificial rhythm; but so long as this is not the case with specimens whose ganglionic function is in a state of normal activity, we must conclude that this function presents some quality which a merely constant stimulation is not able to supply. And this function doubtless consists in supplying a stimulation that is periodic. So that, on the whole, my belief is that the natural rhythm of these tissues—and so, from analogy, of ganglio-muscular tissues in general—is probably due to a double process, of which one part consists in the periodic discharge of the ganglia, and the other in the alternate exhaustion and restoration of excitability of the muscles. No doubt in each species of Medusæ the periods of ganglionic discharge are, as it were, timed to coincide with those during which the exhaustion of the responding tissue remains; so that the ganglionic impulse is always thrown in at the moment when the excitability of the responding tissue is at its climax. In this way nervous energy is doubtless economised, and, if so, the natural rhythm becomes analogous, not to the artificial rhythm as produced by the faradaic current, but to the artificial rhythm as produced by single shocks of minimal intensity thrown in at appropriate periods.

Thus the theory of rhythm which I now propose is not subversive of, but complementary to, the current theory; I merely claim to have proved that over and above the already recognised factor in the production of rhythmic movement of ganglio-muscular tissues there is an additional factor, which, although not hitherto recognised, is probably of at least as much importance.

(*r.*) I may fitly conclude this exposition with a brief reference to the only literature bearing on the subject of artificial rhythm with which I am acquainted. In the 'Journal of Anatomy and Physiology' for July, 1876, there is a paper by Dr. M. FOSTER and Mr. DEW SMITH which details results confirmatory of those which had been previously obtained by ECKHARD and HEIDENHAIN, and which are strikingly analogous to some of those which I have just described. The tissue on which these

four observers experimented was the heart-apex of the Frog. This, in being a muscular tissue deprived of its centres of spontaneity, constitutes a very fair physiological parallel to the paralyzed bell of a Medusa. In the paper alluded to, the authors confine themselves to describing the effects of the constant current in producing rhythmic response on the part of the heart-apex; but in a note previously published by Dr. FOSTER in the same journal (vol. iii., p. 400), it is shown that minimal faradaic stimulation also has the effect of throwing the heart-apex into rhythmic action. The artificial rhythm is not, indeed, so perfect as that which I obtained in the case of *Aurelia*; but it is nevertheless of an unmistakable character. With regard to it Dr. FOSTER makes the following suggestive remark:—"We may infer that the cardiac muscular tissue differs for some reason from ordinary muscular tissue in a disposition towards rhythmic rather than continuous contraction; and that the influence of the ganglia is probably not rhythmic but continuous, whatever the exact nature of that influence may be." And, as already observed, Dr. FOSTER and Mr. DEW SMITH have also obtained rhythmic response to constant stimulation in the case of the Snail's heart.

The only other observation bearing on this subject with which I have met, is one that was published by Dr. BURDEN SANDERSON and Mr. PAGE in the 'Proceedings of the Royal Society.' The tissue on which these observers experimented was the excitable leaf of *Dionæa*, and they were able to show that slightly less than minimal stimulation produces rhythmic response in these tissues. The response in this case was estimated, not by the occurrence of a contraction—the stimulation employed being too feeble to cause any contraction—but by the occurrence of the electrical disturbance which, as these authors have shown, always constitutes the first result of stimulation, and therefore takes place even in cases where the stimulus is not strong enough to cause contraction. The following are the words in which the fact is stated by its observers:—" When a leaf is excited at regular intervals by single shocks of such intensity as to be just beyond the limit of adequacy, so that the slightest diminution would render them futile, it is sometimes observed that the effects become rhythmical. Thus, in a series of 54 successive excitations, we obtained the following results:— Excitations 1, 2, 3, and 4, were effectual; but of the 16 excitations following every other was futile, the alternate ones only being followed by excursions (*i.e.*, of the electrometer); then followed during eight minutes a series of futile excitations, after which the leaf was allowed to rest for two minutes. On resuming, the alternate rhythm again appeared for six excitations, then becoming modified, so that an excursion followed every fourth instead of every third excitation, a state of things which continued for a quarter of an hour."

Thus, then, as a final result, we see that, not only in the case of the lowest organisms, and not only in the case of the paralyzed tissues of the Medusæ, and of the Frog's tongue, but also in that of the Frog's heart, the Snail's heart, and of the excitable tissues of the *Dionæa*, there is observable a tendency to a more or less

marked exhibition of rhythmic response under the influence of constant stimulation of low intensity.

§ 2. *Luminous stimulation of the covered-eyed Medusæ.*—In my previous papers I have detailed the results of various experiments on the luminous stimulation of the naked-eyed Medusæ. Since the publication of these papers I have tried whether the covered-eyed Medusæ are likewise susceptible to this mode of stimulation, and I have found that, although the results are not of so marked a character as they are in the case of the naked-eyed Medusæ, nevertheless, by a little care, it does admit of being proved that the lithocysts of the covered-eyed Medusæ resemble the marginal bodies of the naked-eyed Medusæ in being rudimentary organs of vision.

The best way that I have found of proving this fact is to divide an *Aurelia* into segments, leaving one or more lithocysts in each segment. On then choosing a segment which is not very active, and leaving it for some time in the dark, it may be observed, on approaching it with a candle, that its activity is much less pronounced than it was in the daylight. But after the candle has been allowed to shine upon it for a few seconds, the segment begins to become gradually aroused into a state of greater activity. If the lithocyst, or lithocysts, be now removed, the approach of the candle, or the access of daylight, produces no stimulating effect.

§ 3. *Localising movements of the polypite of* Aurelia aurita.—In my previous paper I have fully described certain movements of localisation which are performed by the polypite of a certain naked-eyed Medusa (*Tiaropsis indicans*), whenever any portion either of the polypite itself or of the concave surface of the nectocalyx is stimulated. I have now ascertained that somewhat similar movements are performed, under similar circumstances, by the polypite of *Aurelia aurita*. For if an *Aurelia* be suspended in a large bell-jar of sea-water, so as to admit of the free movement of the polypite in all directions, and if any part of the concave surface of the umbrella be then touched, or otherwise irritated, the two lobes of the polypite which are nearest to the seat of irritation will slowly approximate and close over that point, as if attempting to embrace the irritating body. Sometimes only one lobe will move over to the seat of irritation, but it is more usual for two, or even more, of the four lobes to take part in these localising movements. These movements, however, are not performed with nearly so much activity and precision as they are in the case of *Tiaropsis indicans*; they are, comparatively speaking, of a very sluggish and somewhat uncertain character, never beginning till a number of seconds, perhaps even half a minute, after the application of the stimulus, and the lobes of the polypite then sweeping slowly backwards and forwards over a large area of the umbrella, instead of being quickly and invariably applied to the precise spot that was stimulated.

§ 4. *Effects of alternating the direction of the constant current on the excitable tissues of the Medusæ.*—It is a fact known to physiologists that, in the muscular tissues of the higher animals, the stimulus which is supplied by make and break of the constant current becomes less and less effective as a stimulus the more frequently the current is

passed in the same direction, and that on reversing the direction of the current the stimulations which are supplied by make and break again rise to their original value. (See especially my papers "On the Modification of Excitability produced by Injury," 'Journal of Anatomy and Physiology,' vol. x., and in 'Proceedings of Royal Society,' Nos. 171 and 811.)   I have therefore tried whether these effects admit of being produced in the case of the excitable tissues of the Medusæ, and I find that they are so. I find, further, that these effects admit of being equally well produced whether the current be passed in the direction of the length or in that of the thickness of the muscular fibres.   In other words, the effects in question occur equally well, whether the electrodes be placed on the same radius of the umbrella—so causing the current to traverse the muscle-fibres for the most part transversely—or placed on different, though not widely separated radii, at points equi-distant from the circumference of the umbrella—so causing the current to traverse the muscle-fibres for the most part longitudinally.

II. SECTION.

§ 1.—Allusion has already been made to the fact that in the contractile tissues of *Aurelia* there are frequently to be observed immense differences in the force of the contractions, according as the latter are originated by a strong or by a weak stimulation ; that is to say, while a stimulus which is not below some certain degree of intensity will always start a wave of strong contraction from any point of the tissue area which may be chosen as the seat of stimulation, a weaker stimulus may start a wave of contraction so feeble as to be scarcely perceptible.   In some specimens of *Aurelia* these waves of feeble contraction are more easily produced than in other specimens, and occasionally it happens that they are so feeble as to be only rendered perceptible by raising the tissue above the water and inclining the head at such an angle to their level as admits of the eye receiving the reflection of light which falls upon their glancing surface; as a response to each feeble stimulus a slight change in the glancing, indicative of a slight contraction, may then be observed.

It might reasonably be supposed that such feeble waves of contraction would not present much power of radiating through extensive areas of tissue; but, as a matter of fact, they often travel quite as far and well as do the stronger waves.   Indeed, it not unfrequently happens that they gain strength as they advance; so that in a long strip of tissue—especially if a large piece of the umbrella be left attached to the end remote from stimulation—it may happen that a contractile-wave, when started by a feeble stimulus at one end of the strip, is barely perceptible at that end, while it grows into a tolerably strong contraction towards the other end.

When I first observed the occurrence of these almost imperceptible waves of contraction it appeared to me that they might possibly serve to explain the occurrence of what in my previous paper I called waves of stimulation.   But before I published my previous paper I satisfied myself that such was not the case ; and as the establishment

of this point entailed a number of experiments, I think it is desirable in this con-
cluding paper to state their general result, lest other observers should suppose that the
evidence as to the occurrence of waves of stimulation is vitiated by the occurrence of
these almost imperceptible waves of contraction.

That there is here a very probable source of error opened up is, of course, manifest.
As stated in my previous paper, the proof as to the occurrence of waves of stimulation
is two-fold : First, by stimulating a part of the irritable tissue at a distance from a
lithocyst, too gently to start a visible wave of contraction from that part, a wave of
stimulation may nevertheless be proved to have been started ; for, shortly after apply-
ing the stimulus, the distant lithocyst will discharge its ganglionic influence, so giving
rise to a visible wave of contraction, which starts, not from the seat of stimulation, but
from that of the lithocyst.   Secondly, the invisible wave of stimulation through the
excitable tissue of the umbrella may often be seen to have its passage visibly recorded
by the numerous tentacles which in *Aurelia* fringe the margin of the umbrella—one
tentacle after another successively retracting until the " tentacular wave" of retraction
which started immediately below the seat of stimulation in the umbrella has passed
throughout the whole series of tentacles.   In umbrellas with their lithocysts removed
these tentacular waves course all the way round the margin without exciting any
visible contraction in the umbrella-tissue which was the immediate seat of stimulation ;
but if any of the lithocysts are left *in situ*, they invariably discharge their ganglionic
influence shortly after a tentacular wave reaches them.

These facts, of course, tend to show that in the excitable tissues of *Aurelia* there
is some element which performs the essential function of nerve—the function, namely,
of conveying stimuli irrespective of the passage of contractile waves.   But in view
of the fact that in these same tissues contractile waves may occur of so feeble an
intensity as to be almost invisible, it becomes necessary to be quite sure that such
waves may not sometimes be so feeble as to be quite invisible, and therefore that what
I have called nervous waves of stimulation are not in reality only invisible muscular
waves of contraction.   The evidence which I have to adduce in order to show that
such is not the case is happily unequivocal.   I cannot, indeed, prove that muscular
waves of contraction may not occur in the excitable tissues of *Aurelia* of too feeble an
intensity to admit of becoming visible ; but I am able to prove that, whether or not
such is the case, other waves of a distinctively nervous kind undoubtedly pass through
these tissues.   The proof of this consists in the fact that sometimes waves of stimu-
lation will continue to pass from one tissue area to another after the passage of
contractile waves between these two areas has been blocked by section ; or, reverting
to the terms employed in my previous paper, excitational continuity may in some
cases remain intact after contractional continuity has been destroyed.   And forasmuch
as it is impossible to suppose that an invisible, or very feeble, wave of contraction can
force a passage where a visible, or very strong, wave of the same kind fails to do so,
the following observations must be regarded as eliminating the possible source of error

with which I am now dealing; they establish the fact that whether or not wholly invisible waves of contraction occur in *Aurelia*, waves of stimulation undoubtedly occur. For the sake of brevity I shall quote these observations from my notes *verbatim* :—

" An *Aurelia* of medium size. One half of the margin removed in the form of a strip two inches broad, the remainder of the umbrella being left attached. After some overlapping sections had completely and permanently destroyed contractional continuity in the strip, excitational continuity clearly remained intact, as shown by the occurrence of a decided tentacular wave at the opposite side of the umbrella whenever the free end of the strip was irritated. That contractional continuity had in this case been effectively destroyed was proved by tetanising the free end of the strip four hours after the section with strong faradaic currents, and also with spirit. Under the influence of such strong stimulation of the free end of the strip, the lobes of the polypite violently writhed, although the umbrella remained quiescent."

This response on the part of the polypite is of conclusive value as proving the occasional persistence of excitational continuity after contractional continuity has been destroyed. My notes contain the record of several other observations confirmatory of this fact, but it is needless to quote them at length. The writhing movements of the polypite under these circumstances are often very decided; but they are usually wonderfully late in beginning. This is probably owing to the prolonged and uncertain period of latency which, as stated in my previous paper, is manifested by the polypite of *Aurelia*; for even in experiments where the contractional continuity of the umbrella tissue has not been destroyed by section, the response of the polypite to strong stimulation of these tissues does not begin till after the violent contractions of the umbrella have been in progress for a considerable time.

§ 2. *Effects of Exhaustion in impeding the passage of contractile waves.*—In my various modes of section of *Aurelia* I have several times observed a fact that is worth recording. It sometimes happens that when the connecting isthmus between two almost severed areas of excitable tissue is very narrow, the passage of contractile waves across the isthmus depends upon the freshness, or freedom from exhaustion, of the tissue which constitutes the isthmus. That is to say, on faradising one of the two tissue areas which the isthmus serves to connect, the resulting contractile waves will at first pass freely across the isthmus to spread all over the other tissue area; but after several such waves have passed in rapid succession across the isthmus, it may happen in some preparations that every now and then a contractile wave fails to pass across the isthmus. When this is the case, if the stimulation is still continued, a greater and greater proportion of waves fail to pass across the isthmus, until perhaps only one in every five or six waves become propagated from the one area to the other. If now single induction shocks be substituted for the faradaic stimulation, it may be found that by leaving an interval of four or five seconds between the successive shocks, every wave that is started in the one area will be propagated across the

isthmus to the other area. But if the interval between the successive shocks be reduced to two or three seconds, every now and then a wave will fail to pass across the isthmus. And if the interval be still further reduced to one second, or half a second, comparatively few of the waves will pass across. Now, however, if the tissue be allowed five minutes' rest from stimulation, and the single shocks be thrown in at one second's intervals, all the first six or ten waves will pass across the isthmus, after which they begin to become blocked as before. It may be observed also that when the waves are thus blocked, owing to exhaustion of the connecting isthmus, they may again be made to force a passage by increasing the intensity of the stimu- lation, and so giving rise to stronger waves having a greater power of penetration. Thus, on re-enforcing the electrical stimulus with the simultaneous application of a drop of spirit, the resulting waves of contraction are almost sure to pass across the isthmus, even though this has been exhausted in the manner just described.

§ 3.—Another fact, which I have several times observed during my sections of *Aurelia*, also deserves to be recorded. I have observed it under several modes of section, but it will be only necessary to describe one observation.

Fig. 11.
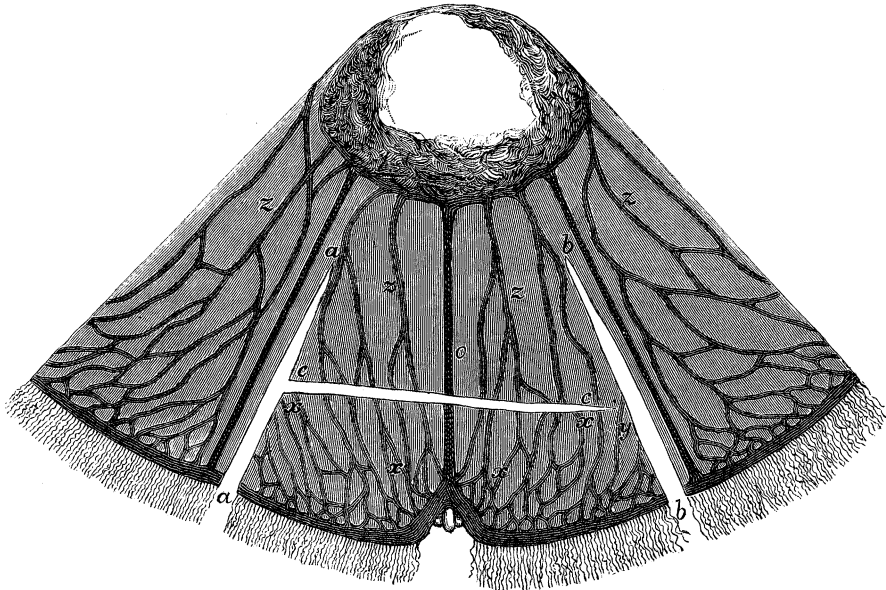
In the *Aurelia*, of a portion of which the accompanying woodcut is a representation, seven of the lithocysts were removed, while the remaining one was almost entirely isolated from the general contractile tissue by the incisions *a a*, *b b*, *c c*. The lithocyst continued to animate the tissue area *x x x x*, and through the connecting passage *y* the contractile waves spread over the remainder of the subumbrella tissue *z z z z*. So far, of course, the facts were normal; but very frequently it was observed that the contractile waves did not start from the lithocyst, or from the area *x x x x*, but

from the point o in the area $z\,z$.   After this origination of the contractile waves from the point o had been observed a great number of times, I removed the lithocyst. The effect was not only to prevent the further origination of contractile waves in the area $x\,x\,x\,x$, but also to prevent their further origination from the point o—the entire umbrella thus becoming paralyzed.   Hence, before the removal of the lithocyst, the contractile waves which originated at the point o, no less than those which originated at the lithocyst itself, must in some way or other have been due to the ganglionic influence emanating from the lithocyst and asserting itself at the distant point o.

This property which lithocysts sometimes present of asserting their ganglonic influence at a distance from their own locality, can only, I think, be explained by supposing that at the point where, under these circumstances, the contractions originate, there are situated some scattered ganglionic cells of considerable functional power, but yet not of power enough to originate contractile waves unless re-enforced by some stimulating influence which reaches them from the lithocyst through the nervous plexus.   But whether or not this is the true interpretation of the facts, I think it is evident that these facts are of considerable importance in relation to the theory of ganglionic action which has already been so fully discussed in the first division of the present paper.   For, turning again to the woodcut (fig. 11), if the discharges of the lithocyst are regulated only by resistance, it seems almost unaccountable that these discharges should frequently fail to excite the contiguous area $x\,x\,x\,x$, while they are effectual in exciting the remote area $z\,z\,z\,z$; and this even after $z\,z\,z\,z$ has been almost completely severed from $x\,x\,x\,x$ by the severity of the incisions.   To my mind, the facts seem rather to point to the conclusion that the lithocyst is engaged in emitting some sort of continuous ganglionic impulse which spreads throughout the nervous plexus, and helps to stimulate the ganglionic cells which are scattered throughout this plexus.   And this conclusion is not incompatible with the view that the resistance which is offered by the plexus is so adjusted to the accumulation of energy by the lithocyst, that this energy admits of being periodically discharged in greater amount, just at the time when the contractile tissues have completely recovered from their exhaustion due to their previous contraction.   In support of this interpretation of the facts, it may be added that after the removal of the lithocyst I tried the effects of gently irritating the tissue in the area $x\,x\,x\,x$ with a camel-hair pencil, and I found that by so doing I could again excite the origination of contractile waves from the point o in the area $z\,z\,z\,z$.

§ 4. *Regeneration of the excitable tissues of* Aurelia aurita.—The only remaining facts which I have now to communicate have reference to the astonishing rapidity with which the excitable tissues of the Medusæ regenerate themselves after injury. In this connexion I have mainly experimented on *Aurelia aurita,* and shall therefore now confine my remarks to this one species.

If with a sharp scalpel an incision be made through the tenuous contractile sheet of the subumbrella of *Aurelia,* in a marvellously short time the injury is repaired.

Thus, for instance, if such an incision be carried across the whole diameter of the sub-umbrella, so as entirely to divide the excitable tissues into two parts while the gelatinous tissues are left intact, the result of course is that physiological continuity is destroyed between the one half of the animal and the other, while the form of the whole animal remains unchanged; the much greater thickness of the uninjured gelatinous tissues serving to preserve the shape of the umbrella. But although the contractile sheet which lines the subumbrella is thus completely severed throughout its whole diameter, it again re-unites, or heals up, in from four to eight hours after the operation.

For a more careful study of this process of healing I adopted the following mode of section. With a pair of scissors I cut out the ovaries of the animal, so converting the latter into a broad open ring. This ring I then cut through by means of a single radial cut, thus converting the *Aurelia* into a single broad band. With a sharp scalpel I now carried an incision across this band, taking care only to sever the thin layer of excitable tissue, while leaving the gelatinous tissue uncut. The first effect of the operation was that of making the two edges of the excitable tissue to gape apart from one another, so revealing the clear underlying gelatinous tissue.* Physiological continuity was, of course, immediately destroyed at the line of incision. But after an hour or two a slight tumefaction of the gelatinous tissue caused the gaping in the excitable tissue to become less marked, and eventually the edges of the latter were by this means brought into apposition. Generally in about six hours after the operation some part or parts of the incision through the excitable tissue had become sufficiently healed up to admit of the re-establishment of physiological continuity between the previously discontinuous parts of the strip—contractile waves now coursing all the way along from end to end of the strip. At this stage it might be observed that as each wave of contraction passed across the line of incision, the parts of that line which had not yet adhered together gaped away from each other. But the healing process rapidly continuing, adherence rapidly extended along the whole line of incision, and generally in from twelve to twenty hours this adherence was complete. By observing carefully, however, there might still be seen a cicatrix marking out the line of previous incision, though in the course of next day this too disappeared, leaving no trace behind of the previous injury.

It is an unfortunate circumstance that I found it impossible to procure any microscopical preparations of these lines of incision, owing to the fact that all the hardening and staining reagents immediately caused the newly-healed muscle-fibres again to rupture. After many trials I was therefore at last obliged to satisfy myself with an examination of the newly-healed tissues in their fresh state. I was particularly anxious to ascertain whether the physiological continuity which was thus re-established through narrow necks of tissue depended for its re-establishment upon the regeneration

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* "Underlying," because to perform the operation the umbrella requires to be placed with its concave, or excitable, surface uppermost.

of nerve-fibres or only upon that of muscle-fibres. But owing to the impossibility of procuring a stained preparation of such a regenerated injury, I cannot speak with confidence upon this point. I can only say that the nerves which admit of being seen without staining never pass across the line of incision till long after the contractile waves are able to do so. But, of course, this does not prove that the more delicate nerves which are only brought into view by staining may not have previously passed across the line of incision, and have thus been instrumental in the re-establishment of physiological continuity.

I may here observe that, so far as my experiments in this connexion have gone, it appears to be an essential condition to the regeneration of the excitable tissues that the whole thickness of the gelatinous tissues should not have been severed. That is to say, I have never succeeded, though I have made a number of trials, in obtaining union between any two parts of a Medusa which have been completely severed from one another and are then held in close apposition by stitching. So far as I have seen, it is only when the gelatinous tissues of the umbrella are left intact, or, at least, are not severely injured, that the injuries in the excitable tissues will admit of being repaired.

III. GENERAL SUMMARY.

Artificial rhythm may be produced in various species both of covered- and of naked-eyed Medusæ, though in some species electrical and in other species chemical stimulation is most effective for this purpose. In all cases, however, the stimulation which is supplied must be constant and of not more, or but slightly more, than minimal intensity. In *Aurelia* artificial rhythm is best produced by employing weak faradaic stimulation, when the resulting rhythm is often of a most regular and persistent character. Eventually, however, exhaustion produces irregularity and cessation of the rhythm, and prolonged rest is then required before any perfect rhythm can be again produced by the faradaic stimulation. Increasing the strength of the current within certain limits increases the rate of the rhythm. In *Sarsia* artificial rhythm may be best produced by employing weak chemical stimulation. Soon after the concave surface of the paralyzed bell becomes opalescent, the shivering movements begin, and continue without intermission for a variable time. Shortly after transference of the bell to normal sea-water these movements cease, to be again resumed if the bell is again transferred to acidulated water. The paralyzed bell of *Sarsia* will sometimes manifest these rhythmic movements even in normal sea-water, provided that it has first been injured by the application of either the constant or the induced current. The polypite of *Sarsia* will also manifest a slow and long-continued rhythm as a result of mechanical or chemical injury. The umbrella of *Aurelia* will sometimes give three or four rhythmic contractions in response to a single mechanical stimulation, and will sometimes also respond rhythmically to the constant current. Thus all modes of constant stimulation (except heat) may produce artificial rhythm in one or other of these two species of Medusæ.

The explanation which I have offered to account for the phenomena of artificial rhythm is, that an alternate process of exhaustion and restoration of excitability on the part of the contractile tissues causes the constant stimulation of minimal intensity alternately to fall below and to rise above the limits of adequacy. This explanation has been tested and supported by various experiments, which it is not necessary again to detail. Taking, therefore, this explanation of the artificial rhythm as satisfactory, it follows that it probably has an important bearing on the facts of natural rhythm. For if in the production of artificial rhythm the exhaustion of contractile tissues is found to play so essential a part, it becomes incredible that it should not likewise play some part in the production of natural rhythm. I am therefore led to suppose that in all ganglio-muscular tissues which present rhythmic movement, the rhythm is not exclusively due to any resistance mechanism on the part of the ganglionic tissues, but that it is at any rate in large measure due to this alternate rise and fall of excitability on the part of the muscular tissues. And I have submitted that this view is sustained, à priori, by the fact that rhythmic action is of the most frequent occurrence in lowly organized tissues where as yet there has been no segregation of ganglionic structure, and, à posteriori, by the fact that in Sarsia the same ganglia supply at the same time a stimulus to the rhythmic action of the lowly excitable tissues of the bell, and a stimulus to the tonic action of the more highly excitable tissues of the polypite. And, as additional facts confirmatory of the same view, I have also cited the observations of ECKHARD, HEIDENHAIN, FOSTER, and DEW SMITH on the rhythmic action of the heart-apex under the influence of the constant current; the observations of Dr. FOSTER on the rhythmic action of the same tissue under the influence of the faradaic current; his observations on the phenomena of artificial rhythm as they occur in the Snail's heart; the observations of Dr. BURDON SANDERSON and Mr. PAGE on the rhythmic properties of the excitable tissues of Dionæa; and my own observations on the rhythmical motions of the Frog's tongue. But in thus suggesting some modification in the current theory of ganglionic action, I have been careful to state that I do not attempt to overturn, but merely to supplement it. I think I have shown that the theory in question is inadequate to account for all the facts, and that in order to render it a complete theory, we must recognise, not only a periodicity of stimulation on the part of the ganglionic tissues, but also an inherent tendency to rhythmic action on the part of the responding tissues.

Light has been shown to act as a stimulus on the lithocysts of the covered-eyed Medusæ.

The polypite of Aurelia aurita has been shown to perform localising movements somewhat similar to those which are performed by the polypite of Tiaropsis indicans, though the localising movements are of a much more sluggish and uncertain character in the former than in the latter species.

The effects of alternating the direction of the constant current on the excitable tissues of the Medusæ has been shown similar to those which occur in the muscular

tissues of the higher animals, and this whether the current be passed in the direction of the length or in that of the thickness of the muscular fibres.

Waves of contraction in the excitable tissues of *Aurelia*, when started by a very weak stimulus, may be so feeble as to be barely perceptible. This fact in itself raises the presumption that the so-called waves of stimulation, which were described in my former paper, may really be but waves of contraction which are too feeble to be perceptible at all; and hence that the phenomena of reflex action, &c., as they occur in the Medusæ may be due, not to nerve, but to muscle. This presumption, however, is excluded by the additional fact that very often severe section of the excitable tissues has the effect of completely blocking even the strongest waves of contraction while still allowing the waves of stimulation to pass freely, as shown by tentacular waves, reflex action of the lithocyst, and writhing response of the polypite continuing to assert themselves beyond the region in which the contractile waves have been blocked by section.

Exhaustion of a narrow isthmus of junction tissue sometimes has the effect of blocking the passage of contractile waves in that isthmus, their passage, however, being resumed when the junction tissue is allowed time to recover its full excitability.

It has been several times observed that the ganglionic influence of a lithocyst admits of asserting itself at a distance from the seat of the lithocyst itself, and this even when severe forms of section are interposed between the lithocyst and the distant point in the tissue at which the contractile waves are originating. The interpretation of this fact need not again be rendered.

It has been uniformly observed that the contractile tissues of *Aurelia*, after having been completely severed with a sharp scalpel, in from four to eight hours regenerate themselves sufficiently to admit of the re-establishment of physiological continuity across the line of previous severance.

IV. LITERATURE.

I shall terminate this concluding paper on the locomotor system of Medusæ with as brief a reference as possible to the existing literature of the subject. In my first paper I have already had occasion to render an epitome of the memoirs of Professors AGASSIZ and HÆCKEL, so that it becomes needless in this place again to state the results at which these observers arrived. Neither is it desirable to discuss in this place the results which were arrived at by the numerous observers prior to the date of Professor HÆCKEL's work. It is not desirable to do so, because these results, in so far as they professed to be positive, were for the most part erroneous, and in so far as they were combative of error, now possess only an historical interest. Those who may care to consult the literature of this subject on account of any such interest which it may have for them, will require more particularly to consult the following works :—

EHRENBERG, 'Die Acalephen des rothen Meeres und der Organismus der Medusen der

Ostsee,' Berlin, 1836; KÖLLIKER, 'Ueber die Randkörper der Quallen, Polypen und Strahlthiere,' FRORIEP's neue Notizen, bd. xxv., 1843; VON BENEDEN, "Mémoire sur les Campanulaires de la côte d'Ostende," 'Mémoires de l'Académie de Bruxelles,' vol. xvii., 1843; DESOR, "Sur la géneration medusipare des Polypes hydraires," 'Annales d. Scienc. Natur. Zool.,' ser. iii., t. xii., p. 204; KROHN, "Ueber Podocoryna carnea," 'Archiv. f. Naturgeschichte,' 1851, b. i.; McCRADY, "Description of Oceania, &c.," 'Proceedings of the Elliot Society of Natural History,' vol. i., 1859; L. AGASSIZ, "Contributions to the Acaliphæ of North America," 'Memoirs of the American Academy of Arts and Sciences,' vol. iii., 1860, vol. iv., 1862; LEUCKART, 'Archiv. f. Naturgeschichte,' Jahrg. 38, b. ii., 1872; HENSEN, "Studien über das Gehörorgan der Decapoden," 'Zeitschr. f. wiss. Zool.,' bd. xiii., 1863; SEMPER, " Reisebericht," ' Zeitschr. f. wiss. Zool.,' bd. xiii., u. xiv.; CLAUS, "Bemerkungen über Clenophoren und Medusen," 'Zeitschr. f. wiss. Zool.,' bd. xiv., 1864; ALLMAN, "Note on the Structure of Certain Hydroid Medusæ," Brit. Assoc. Rep., 1867; FRITZ MÜLLER, "Polypen und Quallen von S. Catharina," 'Archiv. f. Naturgesch.,' Jahrg. 25, bd. i., 1859; also " Ueber die Randbläschen der Hydroidquallen," 'Archiv. f. Anatomie und Physiologie,' 1852.

A brief sketch of the contents of these and other memoirs on the histology of the Medusæ is given in Drs. HARTWIG recently published work on the nervous system and sense organs of the Medusæ, and these authors point to the important fact that before the appearance of HÆCKEL's memoir, LEUCKART was the only observer who spoke for the fibrillar character of the so-called marginal ring-nerve; so that in HÆCKEL's researches on *Gergonia*, whereby both true ganglion cells and true nerve-fibres were first demonstrated as occurring in the Medusæ, we have a most important step in the histology of these animals. HÆCKEL's results in these respects have since been confirmed by CLAUS, 'Grundzüge der Zoologie,' 1872; ALLMAN, ' A Monograph of the Gymnoblastic or Tubularian Hydroids,' 1871; HARTING, "Notices Zoologiques," Niederlandisches 'Archiv. f. Zool.,' bd. ii., Heft 3, 1873; F. E. SCHULZE, ' Ueber den Bau von Syncorzne Sarsü;' O. and R. HERTWIG, ' Das Nervensystem und die Sinnes-organe der Medusen;' and possibly also by EIMER in his forthcoming publication.

Of these memoirs by far the most important is that of Drs. HERTWIG. These authors state that their investigations were completed before the physiological investigations of Dr. EIMER and myself had fallen under their notice; so that, as they remark, the agreement of their morphological with our physiological results is rendered by this independence the more valuable. In the present paper it will be impossible for me to render a full account of the important work which all scientific naturalists will consult for themselves. I will therefore confine myself to epitomising the lucid epitome which Drs. HERTWIG give of their own histological results.

There is so great and fundamental a difference between the nervous system of the naked- and of the covered-eyed Medusæ, that a simultaneous description of the nervous system in both groups is not by these authors considered practicable. Beginning, therefore, with the naked-eyed division, they describe the nervous system as here con-

sisting of two parts, a central and a peripheral. The central part is localised in the margin of the swimming-bell, and there forms a "nerve-ring" which is divided by the insertion of the veil into an upper and a lower nerve-ring. In many species the upper nerve-ring is spread out in the form of a flattish layer, which is somewhat thickened where it is in contact with the veil. In these species the nerve-ring is only indistinctly marked off from the surrounding tissues. But in other species the crowding together of the nerve-fibres at the insertion of the veil gives rise to a considerable concentration of nervous structures; while in others, again, this concentration proceeds to the extent of causing a well-defined swelling of nervous tissue against the epithelium of the veil and umbrella. In the Geryonidæ this swelling is still further strengthened by a peculiar modification of the other tissues in the neighbourhood, which has been previously described by Professor HÆCKEL. In all species the upper nerve-ring lies entirely in the ectoderm. Its principal mass is composed of nerve-fibres of wonderful tenuity, among which are to be found sparsely scattered ganglion cells. The latter are for the most part bipolar, more seldom multipolar. The fibres which emanate from them are very delicate, and, becoming mixed with others, do not admit of being further traced. Where the nervous tissue meets the enveloping epithelium it is connected with the latter from within, but differs widely from it; for the nerve-cells contain a longitudinally striated cylindrical or thread-like nucleus which carries on its peripheral end a delicate hair, while its central end is prolonged into a fine nerve-fibre. There are, besides these, two other kinds of cells which form a transition between the ganglion and the epithelium cells. The first kind are of a long and cylindrical form, the free ends of which reach as far as the upper surface of the epithelium. The second kind lie for the most part deep under the upper surface. They are of a large size, and present, coursing towards the upper surface, a long continuation, which at its free extremity supports a hair. In some cases this continuation is smaller, and stops short before reaching the outer surface. Drs. HERTWIG observe that in these peculiar cells we have tissue elements which become more and more like the ordinary ganglion cells of the nerve-ring the more that their long continuation towards the surface epithelium is shortened or lost, and these authors are thus led to conclude that the upper nerve-ring was originally constituted only by such prolongations of the epithelium cells, and that afterwards these prolongations gradually disappeared, leaving only their remnants to develop into the ordinary ganglion cells already described.

Beneath the upper nerve-ring lies the lower nerve-ring. It is inserted between the muscle tissue of the veil and umbrella, in the midst of a broad strand wherein muscle-fibres are entirely absent. It here constitutes a thin, though broad, layer which, like the upper nerve-ring, belongs to the ectoderm. It also consists of the same elements as the upper nerve-ring, viz.: of nerve-fibres and ganglion cells. Yet there is so distinct a difference of character between the elements composing the two nerve-rings that even in an isolated portion it is easy to tell from which ring the portion has been taken. That is to say, in the lower nerve-ring there are numerous nerve-fibres of con-

siderable thickness which contrast in a striking manner with the almost immeasurably slender fibres of the upper nerve-ring. A second point of difference consists in the surprising wealth of ganglion cells in the one ring as compared with the other.

Thus, on the whole, there is no doubt that the lower nerve-ring presents a higher grade of structure than does the upper, as shown not only by the greater multiplicity of nerve-cells and fibres, but also by the relation in which these elements stand to the epithelium. For in the case of the lower nerve-ring the presumably primitive connexions of the nervous elements with the epithelium is well-nigh dissolved—this nerve-ring having thus separated itself from its parent structure, and formed for itself an independent layer beneath the epithelium. The two nerve-rings are separated from one another by a very thin membrane, which, in some species at all events, is bored through by strands of nerve-fibres which serve to connect the two nerve-rings with one another.

The peripheral nervous system is also situated in the ectoderm, and springs from the central nervous system, not by any observable nerve-trunks, but directly as a nervous plexus composed both of cells and fibres. Such a nervous plexus admits of being detected in the subumbrella of all Medusæ, and in some species may be traced also into the tentacles. It invariably lies between the layer of muscle fibre and that of the epithelium. The processes of neighbouring ganglion-cells in the plexus either coalesce or dwindle in their course to small fibres; at the margin of the umbrella these unite themselves with the elements of the nerve-rings. There are also described several peculiar tissue elements, such as, in the umbrella, nerve-fibres which probably stand in connexion with epithelium-cells; nerve-cells which pass into muscle-fibres, similar to those which KLEINENBERG has called neuro-muscular cells; and in the tentacles neuro-muscular cells joined with cells of special sensation (Sinneszellen).

No nervous elements could be detected in the convex surface of the umbrella, and it is doubtful whether they occur in the veil.

In some species the nerve-fibres become aggregated in the region of the generative organs and in that of the radial canals, thus giving rise in these localities to what may be called nerve-trunks. But in other species no such aggregations are apparent, the nervous plexus spreading out in the form of an even trellis-work.

In the covered-eyed Medusæ the central nervous system consists of a series of separate centres which are not connected by any commissures. These nerve-centres are situated in the margin of the umbrella, and are generally eight in number, more rarely twelve, and in some species sixteen. They are thickenings of the ectoderm, which either enclose the bases of the sense-organs, or only cover the ventral side of the same. Histologically they consist of cells of special sensation, together with a thick layer of slender nerve-fibres. Ganglion-cells, however, are absent, so that the nerve-fibres are merely processes of epithelium-cells.

Drs. HERTWIG made no observations on the peripheral nervous system of the covered-eyed Medusæ; but they do not doubt that such a system would admit of

being demonstrated, and in this connexion they cite the observations of CLAUS, who describes numerous ganglion-cells as occurring in the subumbrella of *Chrysaora*. It is needless to remark how fully the anticipations of these authors have in this respect been realised by the researches of Mr. SCHÄFER.

Lastly, these authors compare the nervous system of the naked-eyed with that of the covered-eyed Medusæ, with the view of indicating the points which show the latter to be much less completely developed than the former. These points are, that in the nerve-centres of the covered-eyed Medusæ there are no true ganglion-cells, or only very few ; that the mass of the central nervous system is very small, so that all the nerve-centres taken together contain far fewer nerve-fibres than do the nerve-rings of the naked-eyed Medusæ ; and that the centralization of the nervous system is less complete in the covered-eyed than it is in the naked-eyed Medusæ, as shown by the multiplication of similarly formed nerve-centres which occurs in the latter group.

In this memoir the authors also supply an interesting description of the structure of the sense organs in various species of Medusæ ; but it seems scarcely necessary to extend the present *résumé* of their work by entering into this division of their subject.

Within the last few weeks Drs. HERTWIG have supplemented the work which I have thus briefly epitomised with another valuable contribution to the morphology of the Medusæ. This is entitled ' Der Organismus der Medusen und seine Stellung zur Keimblättertheorie.' As, however, this memoir has no special relation to the locomotor system of the Medusæ, it does not appear to require in this paper any special consideration.