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THE RHYTHM AND INNERVATION OF THE HEART OF THE SEA-TURTLE.

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THE present paper is intended in part as a continuation of a shorter one which appeared in Nos. 4, 5, 6, of vol. v. of the *Journal of Physiology* on the same subject; but more especially as a continuation of my work on Chelonian heart physiology in general. So far as I know there does not exist in physiology a *systematic* comparison of the resemblances and differences of any one family or genus. I propose therefore to do for the Chelonians in physiology, to some extent at least, what has been done for them in morphology.

It has hitherto been believed that animals resembling each other in structure closely were similar in physiological behaviour. Such, however, has been rather assumption than the outcome of careful comparison.

With the view of discharging this task of systematic physiological comparison, I have during this past summer made a large number of experiments on various species of sea-turtles at the Marine Laboratory of the Johns Hopkins University at Beaufort in N. Carolina; and also a limited number of experiments on the land-turtle. I desire to express my thanks to Dr Brooks, professor of morphology in the Johns Hopkins University for his kindness in facilitating my work.

The marine turtle has much less vitality than other Chelonians, and suffers when kept for a few days out of the water or deprived of its proper food. In order that my animals should be in the best possible condition, a matter of special importance in connection with the subject of spontaneous rhythm, a structure known locally as a "turtle pen" was constructed on the sea shore, of dimensions 12 × 8 × 8 feet, admitting water freely, and so placed that the animals were never without a certain amount of water at the lowest tide. As learned from a fisherman who made a specialty of catching sea-turtles, their principal food consists of crabs. Upon such those kept for a few days in confinement were regularly fed. Most of the animals upon which I have worked were not kept in the pen for longer than two to four days.

According to Holbrook's work on American Reptilia the three species of marine turtle used in my experiments were *Chelonia caretta* or the Loggerhead, *Chelonia imbricata* or Hawksbill, and *Chelonia mydas* or the Green Turtle.

The conclusions and observations of this paper are based upon prolonged and careful experiments by the direct method on twenty specimens of the marine turtle.

As in my paper on the heart of the Terrapin the literature of the subject is pretty fully considered, that part will be omitted in this paper, so that it may be kept as short as possible.

For stimulation, as in my work on the Terrapin, a Du Bois inductorium fed by one Daniell's cell was employed.

I. *Spontaneous Rhythm of the different Parts of the Heart.*

The subject is so interesting, and such important conclusions have been drawn regarding it, that I shall give a condensed account of a large number of experiments on this subject.

Exp. I.—*Chelonia imbricata;* caught only twenty-nine hours.

At 10.25 A.M. a ligature placed around the auriculo-ventricular junction; ventricle not arrested till ligature is drawn very tight.

10.28 A.M., 1st beat of ventricle.
10.30 „ 2nd „
10.32 „ 3rd „
10.34 „ 4th „
10.36 „ 5th „
10.38½ „ 6th „
The rhythm never got faster, but gradually subsided.

Exp. II.—*Chelonia imbricata.*

At 11.35 A.M. ligature drawn tightly at junction of sinus with auricle; complete arrest of all parts posterior to the ligature.

1 P.M. After several pricks with a seeker, a succession of beats but no spontaneous rhythm; sinus beats regularly from the first.

2.15 P.M. Ventricle became rigid throughout almost its whole extent. Right auricle much more vitality than left auricle.

3.30 P.M. Not possible by mechanical excitation to call forth a beat in left auricle; right auricle still somewhat excitable.

EXP. III.—*Chelonia mydas*, most lively specimen of any marine turtle I have seen.

At 12.30 A.M. animal bled freely after destruction of brain. Greater part of auricles proper ("bulged" part) cut away; they continue to beat in harmony with the sinus and sinus extension ("basal") or "flattened" portion of Gaskell.

Soon ventricle cut clearly free from the rest of the heart, *i.e.*, no sinus extension adhering. Sinus and auricles act together in sequence and maintain the original rhythm of 32.

12.45 A.M.–12.48 A.M. Ventricle 3 beats.
12.54 „ Ventricle 14 beats in 1 minute.
12.58 „ „ 17 „
12.58 A.M.–1.2 A.M. Several small groups of beats.
1.3 „ Ventricle 8 beats in 1 minute, all grouped.
1.9 „ Ventricle a rhythm of 7 beats 1 minute.
1.10 „ „ 7 „
1.11 „ „ 5 „
1.13 „ „ 16 „
1.14 „ „ 11 „
1.15 „ „ 12 „
1.20 „ „ 12 „
1.25 „ „ 8 „
1.30 „ „ 8 „
2.25 „ „ 4–6 and irregular.

N.B.—2.50 A.M. After a previous pause of several minutes, rhythm began again, at first only at the edges of the ventricle, then grows gradually stronger and spreads over more of the ventricle, but never involves the whole of it.

The last observation is important, as it shows how contraction of certain fibres of the ventricle tend to call into action others, and strengthen those already acting, but weak. Similar cases have been reported for the Terrapin.

The above cited experiment furnishes the best-marked case of spontaneous rhythm I have met.

EXP. IV.—*Chelonia caretta*, about 3 feet long; out of water two days.

1.5 P.M. Ligature between sinus and auricle and sinus extension does not arrest rhythm of auricles and ventricle *till it is drawn very tight.*

No spontaneous rhythm of any part posterior to the ligature.

N.B.—1.30 P.M. On attempting to get the ventricle to pulsate in response to a prick from a seeker it *passes into fibrillar action.* This case presents a great contrast to the previous one, but the animal in the latter case had been out of the water two days, while the other specimen was quite fresh.

Exp. V.—*Chelonia mydas.*

11.10 A.M. Ligatured between ventricle and parts just above; former arrested at once.

12.10 A.M. Ventricle a beat now and then, on an average 1 in the minute, auricles and sinus a rhythm of 30.

1.10 A.M. Ventricle 5 beats in 3 minutes at irregular intervals.

1.50 A.M. Ventricles 3 beats in 4 minutes.

2.50 A.M. Auricles irregular; right beats before left; ventricle 5 beats in 5 minutes.

4 A.M. Ventricle has almost ceased to pulsate, but a touch of the finger suffices to start the ventricle into a rhythm of 24, lasting for two minutes.

This latter observation illustrates well the great *sensitiveness* or excitability of the ventricle of the sea-turtle.

Exp. VI.—*Chelonia mydas;* animal bled to death, after destruction of brain.

1.30. Cut away sinus from auricles, sinus extension, and ventricle; very soon a rhythm arises in the latter parts.

2.10 A.M. Right auricle beats slightly before the left.

2.40 A.M. Left auricle beats only feebly; ventricle getting rigid.

3.10 A.M. Ventricle wholly rigid; right auricle beating at rate of 12; left auricle quiescent; vertical section made between the auricles, &c.; right auricle continues to beat.

Exp. VII.—*Chelonia imbricata.*

10 A.M. Cut away side ventricle from rest of heart; then the auricles proper from the sinus extension and the ventricle free from the parts above it. This gives rise in the ventricle to a rapid rhythm of excitation for a very short time, followed by a rhythm of 1–2 in the minute for 3–4 minutes; rhythm of heart at time of section, 20.

10.15 A.M. Sinus extension a rhythm of 19, and irregular.

10.30 A.M. „ „ 13.

10.45 A.M. „ „ 12.

Ventricles no pulsation throughout.

12 noon. Ventricle rigid; sinus extension a rhythm of 15, and irregular; auricles proper die much later than ventricles, but have no spontaneous rhythm whatever.

This experiment clearly demonstrates the greater tendency to, and capacity for, spontaneous rhythm of the sinus extension (or "basal" or flattened portion of the auricle) than any other part, including the auricles proper.

To state the results of the rest of my experiments would be very much of a repetition of the above; the experiments have been numerous and occupied much time, and justify, I think, the following conclusions for the sea-turtle:—

1. The power of originating spontaneous rhythm is in the order: sinus, sinus extension, auricle, ventricle; that of the sinus being much the best marked.

2. The degree of spontaneous rhythm of the ventricle varies with the species (and individual) and the state of nutrition and general vitality of the animal. This probably applies also to the rest of the heart, but is most conspicuous in the ventricle. *C. mydas* has shown much the greatest capacity for spontaneous cardiac rhythm of the species of marine turtles examined by me.

3. The spontaneous rhythm of the ventricle never equals that of the original rhythm of the ventricle, in fact usually remains very slow indeed.

An examination of the cases reported from my experiments above will show that the ventricle has a purely spontaneous rhythmic tendency, but that this tendency is after all rather feeble.

In all the experiments the heart was left *in situ*, surrounded either by pericardial fluid, blood plasma, or serum, so that its nutrition was provided for.

When ligatures were used a certain quantity of blood was imprisoned necessarily within the cavities thus shut off.

A glass vessel was also placed over the heart, thus forming a moist chamber.

The heart of the marine turtle is much more sensitive to conditions of nutrition than that of either the land tortoise or the Terrapin, which is, of course, an obstacle in the way of the development of spontaneous rhythm.

I have found that unless the ligatures used are somewhat fine and *drawn very tight* a rhythm may arise possibly not equal to the original one, nor to that of the part of the heart usually dominating the rhythm in question (*e.g.*, auricle the ventricle), thus simulating a genuine spontaneous rhythm; while in reality it is in part due to stimulation from the wave of contraction of the part above, the ligature causing a sort of marked "block" only.

With so sensitive a ventricle as that of the marine turtle I am satisfied the attachment of a lever and the effects of the same on the rhythm would be considerable. If feeding the heart could be so regulated that the pressure within its own special arterial system did not exceed the normal it might be unobjectionable; but it is difficult or impossible to ascertain what this *norme* is. I therefore regard results obtained with the attachment to the heart of a recording lever, suspension of the heart and feeding it through its own vessels, except under the conditions defined above, as not those of spontaneous rhythm, but as in part due to excitation; and for these reasons it seems to me my experiments really indicate the amount of genuine spontaneous rhythm of the heart of the Chelonians more nearly than those of Gaskell, in which he has employed suspension, recording levers, and feeding.

At the same time I am inclined to believe that in the land tortoises the ventricle has greater tendency to spontaneous rhythm than in some other kinds of Chelonians.

Since the part of the heart, not sinus proper and not constituting the more prominent part of the auricles, is different in appearance, in structure to some extent, and in function, especially in its spontaneous rhythmic power, as well as conductivity, &c., and inasmuch as it in these respects approximates more closely to the sinus than to the auricle proper, it would, I think, conduce to clearness if this part were considered and called the *sinus extension*. This seems the more natural seeing that a similar structure, manifestly more like the sinus than the auricle, exists in the fish.[1]

Though this division was not clearly defined in my paper on the Terrapin, "auricle" is used in the sense of the auricle proper, or bulged part between sinus and ventricle.

II. *Reflex Cardiac Inhibition.*

The results of my experiments on this subject may be shortly stated as follows:—

1. Prolonged gentle tapping with a forceps over the abdominal organs had less effect than a pushing down movement with a seeker, and still less than a single sharp blow with the forceps.

[1] "On the Structure and Rhythm of the Heart in Fishes," &c., vol. vi. Nos. 4 and 5, *Journal of Physiology*.

2. Stimulation of the brachial plexus, with a strong interrupted current, has not in general produced much slowing of the rhythm. In one case it seemed to quicken it.

3. Sponging over the peritoneum vigorously has generally produced cardiac slowing or arrest.

Peculiar Effects.—1. In certain cases, electrical stimulation of the anus has caused marked arrest of the heart; but in others a preliminary slowing, followed by an accelerated rhythm, while the current is still passing.

2. In certain cases, stimulation of the liver has led to the usual cardiac arrest; but in others acceleration has been the first result and the only one; while in still others acceleration has followed and preceded slowing.

It is to be understood that, in all these cases, the spinal cord and medulla oblongata were intact.

The significance of such results as those cited above are discussed in my paper on the alligator.

Upon the whole it may be said that, while in the matter of cardiac arrest by reflex agency, there is much similarity among the different genera and species of Chelonians, the *Chelonia mydās* is the most susceptible of the three species examined by me; and the Slider Terrapin is almost if not quite equal to it in this respect, and in advance of the other marine turtles. The condition of the animal at the time of experiment is also a most important factor.

III. *Stimulation of the Vagi.*

The possible effects of stimulation of the vagi in the marine turtles are:—

1. Preliminary weakening of the beat, most marked in the auricles, without arrest of the heart's action or change in the rate of beat. This may occur with a very weak current; but more frequent is—

2. Arrest of the auricles; the rest of the heart continuing either with unchanged or a slowed rhythm and weakened beat. Gaskell[1] has stated in his paper on *Testudo Grœco* that he had never seen any evidence that an excitation wave is able to travel

[1] *Journal of Physiology*, vol. iii. Nos. 5 and 6.

from the sinus to the ventricle and cause a ventricular contraction independently of a wave of contraction over both parts of the auricle. The latter statement is at variance with my observations on the Terrapin and still more frequently on the marine turtles. Often, when both auricles proper are arrested by stimulation of the vagi, the rest of the heart, including sinus extension, may beat as usual; and this holds equally well, as I have observed, for the alligator and the fish.

3. Arrest of the heart by diminution of the force of the contractions to zero, as often occurs in the Frog, does *not*, so far as my observations go, occur in any Chelonian.

4. The ventricle with the auricles may cease, the sinus and sinus extension continuing to beat. But such stop is likely to be very brief, the wave of contraction soon passing on.

5. Preliminary acceleration, which is very rare in the S. Terrapin, occurs more frequently in the sea-turtle, but never except with the stimulation of a weak current.

I have noticed brief preliminary acceleration soon followed by slowing, the strength of the current remaining the same, when the heart's powers have been much enfeebled.

Arrest of the sinus, auricles and ventricles continuing to beat, is unknown.

Diastolic relaxation during stimulation is perhaps in the marine turtle rather less marked than in the Terrapin; but it does occur, and equally well in the bloodless heart.

The After-Effects of Vagus Stimulation.—These are very similar in all the Chelonians; in all, stimulation of the vagus may be followed by a rhythm without increase; a rhythm with slight increase or with marked increase; and the same law holds equally well in the sea-turtle as in the Terrapin that *the rate of increase in the force and frequency of the beats of the heart is in inverse proportion to those prevailing at the time of stimulation;* from this it follows that a weak heart, one needing help most, is the one the vagi nerves can actually improve most effectually. This has been illustrated to me over and over again when working on the marine turtles; thus, when, as the heart is getting weak, the left auricle, as is the rule, falls into a condition of great enfeeblement, while the right is comparatively strong, the stimulation of the vagus will restore the left, for a time at least, to harmony of rhythm with its fellow, and produce marked improvement in the strength of the beats.

The after acceleration in the sea-turtles, especially in *C. caretta* and *imbricata* seems to reach its maximum sooner than in the Terrapin. This does not apply equally to *C. mydas,* I think. Further, when the heart is enfeebled in all kinds of Chelonians, the maximum is more rapidly attained, and this remark applies with especial force to the marine turtles.

The beat may recommence after standstill from vagus stimulation, in the order: sinus (always), sinus extension, ventricle, auricles; or in the order: sinus, sinus extension, and auricles, ventricle; and the same holds for the Alligator and the Fish.

Unilateral Effects of Vagus Stimulation.—These have been referred to in my paper on the Terrapin (pp. 249, 250), and relate especially to greater dilation of the auricle, than the other during stimulation of its corresponding nerve. While such dilating effects have been noticed for the sea-turtle, arrest of an auricle answering to the vagus stimulated, has been more frequently observed than in the Terrapin; in several cases this phenomenon has been very pronounced, and has followed on every stimulation of the nerve with a sufficiently *weak current.*

Stimulation of the Central End of one Vagus, the Medulla and the other Vagus being intact.—The results may be stated briefly as follows:—

1. In all the specimens of the sea-turtle examined in this way (with one exception, in which there was doubt as to the soundness of the medulla) either arrest or slowing of the rhythm has followed.

2. In most cases this could be repeated 3 to 6 times at short intervals, but with less and less effect on each occasion. Considering the great vital tenacity of the nerves in the Chelonians, this seems to point to exhaustion of the inhibitory centre.

3. In a certain proportion of cases there is decided after-acceleration (*e.g.*, from 33 to 38 beats).

4. As was seen with the Slider Terrapin, there are great differences in capacity for this form of inhibition in different specimens of the same species.

C. mydas gave much the most pronounced and certain results in my experiments on the marine turtles.

In one instance, with a weak current, preliminary increase in the rhythm occurred, followed by slowing and even short stops of the heart.

Prolonged alternate Stimulation of the Vagi.—The following account of the experiment on this subject furnishes the case of longest cardiac inhibition yet published.

EXP.—*Chelonia imbricata*, 2 feet long.

12.32 P.M. 1. Stimulation of left vagus for 30 minutes, maintains constant standstill; then current withdrawn; after a latency of 14 seconds, rhythm re-established after 1–2 minutes. (First stimulation from 12.32 to 1.3 P.M.)

2. At 1.5 P.M. Stimulation of right vagus till 2.10 P.M.; after the current withdrawn a latency of 16 seconds before rhythm began.

3. Stimulation of left vagus till 3.32 P.M.; when current shut off.

4. At 3.35 P.M. Stimulation of right vagus till 4.25 P.M.; latency 30 seconds.

5. Stimulation of left vagus, from 4.25 P.M. till 6.40 P.M.; when beats began to appear.

Thus in all there was *continuous inhibition of the heart for more than six hours;* for the periods between the stimulation of the right and life vagi were only of sufficient length to ascertain that the heart would still beat, and in none of these cases did the heart begin to pulsate while the current was passing. It was, in fact, evident that the power of the vagus was not exhausted. To this remark the right vagus at 4.26 P.M. is an exception, but in that case the electrodes were at once on the appearance of a beat transferred to the opposite vagus.

It will also be noted that the periods of latency, after the stimulation ceases before a beat appears, lengthens with each stimulation.

Comparative inhibitory power of the two vagi.—The following is the statement of the results in 8 cases :—

Arrest of the heart with the induced current.—

Specimen	I.	Left vagus,	secondary coil	$\frac{1}{2}$ over primary.	
”		Right ”	”	$\frac{3}{4}$ ”	
”	II.	Left ”	”	at 10 c.m. from primary	
”		Right ”	”	5 ” ”	
”	III.	Left ”	”	4 ” ”	
”		Right ”	”	1 ” ”	
”	IV.	Right ”	equal in power.		
”		Left ”			

Specimen	V.	Right	vagus	equal in power.
„		Left	„	
„	VI.	Left	„	inhibits with 2 c. at 3 c.m.
„		Right	„	„ „ 5 cm.
„	VII.	Right	„	„ „ 6 „
„		Left	„	requires the strongest current.
„	VIII.	Left	„	both at 4 c.m.
„		Right	„	

A comparison of these results with those reported for the Terrapin (pp. 247, 248, 249) will show a great resemblance. In by far the larger number of cases the right vagus has greater inhibitory power than the left, exceptions to this, though few, sometimes occurring. In the marine turtle no case in which the left vagus was wholly without effect on the rhythm was found.

This difference between the two vagi, which does not seem to be confined to the Chelonians, but is seen also, as I have shown, in the alligator, calls for explanation. Meyer's [1] explanation, that there were certain cases in which there were no inhibitory fibres in the left vagus, does not agree with facts ; for in all cases the left vagus has some effect either on the force or the rate of the beat. It has been seen that in the Chelonians and alligator arrest of the sinus leads almost invariably to arrest of the rest of the heart, whether that arrest be brought about by the vagus or by a ligature placed between the sinus and auricle; and in those cases in which one vagus is unable to maintain the rest of the heart in standstill, it is always because the sinus is not controlled.

Gaskell [2] has shown that the part of the vagus known as the "coronary" nerve is that which influences the force of the beat of the auricle and ventricle, while the rate depends on the sinus.

The peculiar unilateral vagus effects, pointed out in my paper on the Terrapin, and in this one, seem to me to throw new light on this question.

Beating in harmony with the sinus proper are the terminations of the great veins leading into the sinus. It is easy to see that their conjoined power, which, so to speak, is the *governing* propelling force of the whole heart, is greater, *i.e.*, there is a larger wave of contraction, on the right side than on the left. Now, it is to be observed, that in all those cases in

[1] *Hemmungsnerven System des Herzens*, Berlin, 1869.
[2] *Journal of Physiology*, vol. iii. Nos. 5 and 6.

which the left vagus, under the influence of a weak current, can arrest the left auricle and perhaps the left part of the sinus and its associated veins, that inasmuch as the right part of the sinus keeps pulsating, sooner or later the left part is overcome; whereas, when the right part is arrested its wave is so large, its controlling force so great, the left is of itself so weak, that its wave (also weakened) may not be able to pass on to the sinus extension and auricles; moreover, this left part and its veins, as I have often seen when the heart is dying, ceases to pulsate before the right part of the sinus and its veins. I would then explain the greater effect of the right vagus as a rule by the character of the contraction wave, associated with the right part of the sinus and its associated veins, and by the fact that the nervous supply to this seems to be chiefly from the right vagus, rather than to any deficiency in the kind or number of the inhibitory fibres in the left vagus; both may supply an equal number of such fibres, but if the supply be even partially unilateral, then the results follow as I have endeavoured to explain.

Inasmuch as the force of the auricles is very much lessened by vagus stimulation, great weakening of the beat of the sinus may suffice to arrest the auricles and ventricle without complete arrest of the sinus; in such case sinus arrest is not the sole cause of the stop of auricles and ventricle, nor absolutely essential.

Intracranial Stimulation of the Vagus.—The peculiar inner conformation of the skull of the sea-turtle, and its great thickness and hardness, make examination of the roots of nerves intracranially very difficult. One such examination gave the following results.

Exp.—Rhythm 5–6.

Stimulation of nerve roots from the medulla led to very prolonged inhibition, followed by an accelerated after-rhythm of 7–8.

IV. *Faradisation of the Heart.*

As in the Terrapin, alligator, and fish, the result obtained depends on the strength of the current and the condition of the heart.

The sinus being in good condition, and the current sufficiently strong, it is arrested, but if the heart be much exhausted no arrest may follow; arrest of the sinus of course leads to stoppage of the rest of the heart, unless, as often happens, there is escape of current.

The same arrest of auricles occurs on stimulation, unless the heart be very much exhausted.

Dilation is less prominent in the ventricle of the sea-turtle than in that of the Terrapin; but the bluish appearance accompanying it, and the light points where the electrodes are applied are manifest.

I have never obtained in the sea-turtle arrest of the ventricle by stimulation of this part of the heart with the interrupted current; on the contrary, stimulation of the ventricle gives rise to a more rapid pulsation, or, especially if the nutrition be imperfect, a peculiar form of contraction, which, as it does not exactly resemble that denoted by such terms as fibrillar, peristaltic, &c., I have called intervermiform, which seems preferable to peristaltic, inasmuch as the latter has acquired a very definite physiological meaning, which it is not well to extend.

With a very weak current in all but the freshest hearts the dilation following the stimulation is much more local, and there may be no marked effects as far as rhythmic variation is concerned.

But in a heart very much exhausted it is often quite impossible to arrest the sinus or any part of the heart with the strongest current.

That the white dots seen at the points of application of the electrodes are due to marked contraction of the heart muscle, the behaviour of the alligator's heart renders extremely probable; but that the other effects are due, not to the influence of the current directly on the muscle itself, but indirectly through the nervous mechanisms of the heart, several considerations render highly probable.

1. The effects of the current are very like those of stimulation of the vagus nerve itself, as illustrated above (arrest, dilation, &c.).

2. When the nutrition of the heart is impaired (and its nerves have probably suffered the most), it is impossible to produce the usual effects, arrest of the sinus, auricle, &c.; while at the same

time it is possible to send the ventricle into the peculiar intervermiform action referred to above. This and many other things I have seen, such as the readiness with which even the mammalian heart, long under experiment, &c., goes into a similar action known as the Kronecker-Schmey phenomenon, leads me to believe that this latter also is to be explained, at least in some cases, by peculiar qualities of the muscle rather than through nerve influence; further, in the case of the mammal, this phenomenon and the intervermiform action referred to in the Chelonians, are alike wholly influenced by vagus stimulation.

3. Sponging over the heart arrests it when fresh, while later it may give rise only to intervermiform action on the ventricle; this seems to me a very strong argument in favour of nervous influence.

4. After the free application of atropine to the fish's heart *in situ*, it is impossible to arrest it either by sponging it over or by the application of the electrodes to the sinus; but it is possible to initiate the intervermiform action by this procedure.

V. *Evolution of Function and Cardiac Death.*

In all the Chelonians, the invariable order in which the different parts of the heart die is: (1) ventricle, (2) auricle proper, (3) sinus extension, (4) sinus.

I have studied this subject especially in the sea-turtle, and find that invariably the right auricle outlives the left, and, as has been before indicated, the right moiety of the sinus, and its pulsating venous extensions, tend to outlive the left moiety and its corresponding venous parts.

The death of the ventricle also takes place in a certain segmental order, which is virtually the same in all cases, and which is indicated by dotted lines and numbers (Plate I. fig. 5).

It will be seen from the above figure that the left side of the ventricle dies before the right, and that the last segments to die are a superficial one, extending from the vessels downwards, and another involving the apex, and a portion extending obliquely upwards to the right of it; speaking generally, the *cavum venosum* is the last part of the ventricle to die. From what has been said it appears that as the heart's vitality is being lowered, a more primitive condition of things is reached, *i.e.*, *the heart comes to consist of the sinus, the auricle, and a simplified ventricle*; or to put it otherwise, the parts least dependent on the constant supply of nourishment are those that are oldest in the development of the heart, as those also of greatest independent rhythmic power; so that observation on the order in which any heart dies may be a means of reading its developmental history. It is more difficult to study this subject on the mammalian heart, but Harvey long ago pointed out that the right auricle was the last to die, and that the left ventricle was the first, though he does not seem to have emphasised the significance of this fact.

When in the animal scale among vertebrates a second auricle is acquired, as it is first among the Dipnoï, it is small and of comparatively much less functional importance than the right.

In the sea-turtle not only is the right auricle endowed with greater vitality than its fellow, but it is conspicuously larger, the left, however, making a certain degree of advance as to size on the condition existing in the Dipnoï.

The ventricle in the sea-turtle is much more sensitive to a stimulus than that of other Chelonians; it also has much less vitality, can bear deprivation of its regular nourishment less successfully, as the sea-turtle itself has less vital tenacity than other genera of this family; indeed, there often seems to be associated great vital tenacity of the animal with a corresponding resisting power of the heart, as evinced in the case of *Batrachus tau*, the fish on which my experiments were chiefly made.

VI. *Nerves with Peculiar and Inconstant Influence.*

Reference is made in my earliest communication on the Chelonians[1] to a fine nerve which on the first stimulation produced cardiac arrest followed by acceleration, but the later stimulation of which seemed to be without effect on the rhythm.

I have described what seemed to be accessory vagi in the alligator.

In the sea-turtle I have met with fine nerves traceable upwards towards the superior cervical ganglion and downwards

[1] *Journal of Physiology*, vol. v. Nos. 4, 5, 6.

to the heart, which have acted in a somewhat inconstant manner. Thus sometimes such a nerve has given purely vagus effects; again a first stimulation has caused slowing, and all later stimulations only acceleration; while others again have shown no action beyond the first one, on repeated stimulation. But this I have also noticed to hold for the small accelerating branch from the middle cervical ganglion in the Terrapin. Of course such fine nerves die readily, and are easily exhausted by stimulation; and it may be that the inhibitory fibres in some cases are fewer and are exhausted sooner than the accelerating ones; however, such phenomena, in the present state of our knowledge, are rather puzzling.

Is there a Physiological Depressor Nerve in the Chelonians?— This question has been already answered in the negative by my experiments on the Terrapin. After making two tests on the sea-turtle, the latter of which was in every way satisfactory, the variations in blood pressure being indicated in a rather sensitive way by a simple contrivance, it was impossible to find any fine nerve which produced marked lowering of the blood pressure when stimulated, although very many were tried. Some of the nerves that might be suspected as depressors had a function (peripheral end) which is referred to in the preceding section.

It may then be said that *there is no nerve with the functions of a physiological depressor in the Chelonians.*

VII. *Anatomy of the Sympathetic System of Nerves in the Sea-Turtle.*

The detailed description which I have given of this system for the Terrapin,[1] and which, judging from the account of Gaskell[2] and Gadow, applies largely also to the land Tortoise, may with slight modification be considered as expressing the relations of the sympathetic, vagus, &c., for one species of sea-turtle, viz., *Chelonia mydas.* The resemblance in this respect of this one species to the Terrapin, and its wide divergence from the other species of sea-turtle examined by me, have been very surprising.

[1] *Journal of Physiology*, vol. v. Nos. 4, 5, 6. [2] *Op. cit.*

In *C. mydas* there is the same difference in the size of the sympathetic and the vagus; the same tendency to union for part of their course; the marked distinctness of the ganglion on the main sympathetic stem, &c., seen in the Terrapin, and the figure given in Plate I. (fig. 4) is intended to show in a general way the condition of things present in the Terrapin and *C. mydas*.

But as no satisfactory description for physiological purposes has been published for the marine turtles I shall describe what I have found on the examination of a large number of cases. So much difference has been found in individuals, and the general plan is so disguised, that it was only after considerable examination and comparison that the typical structure could be defined.

In *C. caretta* and *C. imbricata* the great size of the sympathetic in the neck, almost equal to that of the vagus, is in striking contrast with the condition in *C. mydas*, which has the sympathetic scarcely larger than in the Terrapin; also in the two first-mentioned species the vagus and sympathetic run widely apart throughout their whole course; but in *C. mydas*, as in the Terrapin, they sometimes fuse, but not inseparably.

As regards the condition existing at or near the entrance of these nerves into the skull, much difference in details has been found.

In the Loggerhead and Hawksbill there is always more or less fusion above at this point; but in some cases there does not seem to be any genuine blending, for the nerves (vagus, glossopharyngeal, and sympathetic) are separable by a seeker. There is a slight cord-like swelling on the sympathetic, and beyond this two separate divisions enter the skull by different foramina.

In same cases the glossopharyngeal and vagus enter the skull together, and do not seem to have any close connection with the sympathetic.

In these two species I have never found above any such well-defined fusion as exists in the Terrapin and *C. mydas*.

But by far the most remarkable condition found in *C. caretta* and *C. imbricata* is that seen in the third ganglion of the sympathetic stem. It was only after finding a case like that shown in fig. 3 that it became clear that in this ganglion the third and fourth ganglia of the stem were fused together; but when *C. mydas* was examined it was seen that fusion was not, in that species, the rule but the exception, as in the Terrapin.

What is depicted in Plate I. fig. 1 as *ganglion cardiacum basale* must be regarded as the results of the fusion of the inferior cervical ganglion and the first thoracic (G. stellatum).

All of the ganglia except this one are very ill-defined cordiform swellings, scarcely recognisable but for the branches they give off.

The accelerating branch from the middle cervical ganglion is very much more constant, and very much better defined even in *C. mydas* than in the Terrapin. The branch has not in my specimens ever been paired.

The vagus ganglion on its main stem is slightly better marked than the one corresponding to it on the sympathetic. It gives off a very great number of strong branches to parts below (fig. 2).

The brachial plexus in the sea-turtle is exceedingly strong, and forms an interlacement of great complexity. The branches proceed from the fifth–sixth metamere to the ninth.

From the ganglion cardiacum basale several strong branches proceed upwards to the different parts of the brachial plexus, and downwards to various parts, some of them probably to the heart.

VIII. *Cardiac Acceleration by stimulation of the Sympathetic.*

1. Stimulation of the sympathetic above the middle cervical ganglion produces no decided and constant effects on the cardiac rhythm; but influences the eye as in the Terrapin and land tortoise, *i.e.*, the lower lid is depressed and the upper lid elevated; at the same time the pupil is moderately dilated. In consequence of the imperfect development of the nictitating membrane in the sea-turtles, little effect is seen on this structure; the dilation of the pupil has seemed to me to be less marked than in the Terrapin. It has now been shown that in all the Chelonians the main sympathetic has throughout similar functions, not only on the heart but on the eye.

2. Stimulation of the branch from the middle cervical ganglion has produced more constant effects than the corresponding one in the Terrapin; but generally the increase in force of the cardiac beat has been greater than the increase in rate.

3. Stimulation of the ganglion cardiacum basale, or the main stem beyond it, to the next metamere below gives decided accelerating effects.

I have thought that stimulation of branches from this ganglion connected with the brachial plexus had accelerating effects, but of this I do not feel quite certain. The same laws as have been laid down for vagus acceleration apply in this case, especially the law of inverse proportion.

IX. *Further comparison of the Chelonians.*

By way of comparison I have made a series of experiments on a limited number of specimens of one genus of land tortoise (*Pyxis*).

In most respects the heart of this tortoise behaves more like that of the Terrapin than of the sea-turtle. The heart's general appearance is also more like that of the former. In the sea-turtles some species have the ligament at the apex of the heart very highly developed, fibrous bands extending often half way up the ventral surface of the ventricle; and with great breadth of apical attachment. The ventricle is also in the sea-turtles paler, of less vitality and much more sensitive, as before pointed out, than in the other Chelonians.

In the specimens of the land tortoise examined by me the holding power of the left vagus has been less than the right, and I think such differences are better marked than in the water tortoises or marine turtles.

The superiority of the right auricle has been better shown in the marine turtles than in the other Chelonians I have studied.

The independent rhythmic tendencies are greater in the land tortoise, I am inclined to believe, than in most other Chelonians.

The land tortoise and Terrapin resemble each other more than they do the marine turtles in the amount of dilation following direct faradisation of the heart; also neither the Terrapins nor the land tortoise's heart enter with the same facility into intervermiform action as the sea turtle's.

Prolonged stimulation of the vagus has not led, in the land tortoise, to such pronounced results, as regards cardiac inhibition, in the few cases examined by me, as in other Chelonians.

The Chelonians constitute morphologically a very compact group, and it will be seen that the resemblances in the physiological behaviour of this group is in accord with their anatomical likeness. It has been pointed out several times that *C. mydas* is physiologically more closely related to the Terrapin than the other species of sea-turtle I have studied; and it is in this one that the most anatomical resemblance, as far as the cardiac nerves are concerned, is found.

Throughout this paper differences in the physiological behaviour of different species and genera of Chelonians have been pointed out, but it must be remarked that many minor differences, readily discernible by the eye but not easily expressed in words, have been noticed during the year over which these investigations have extended.

The explanation of the different action of drugs on animals closely related anatomically may possibly be reached by some such comparison as I have endeavoured to carry out for the Chelonians.

MONTREAL,
October 1, 1885.

EXPLANATION OF PLATE I.

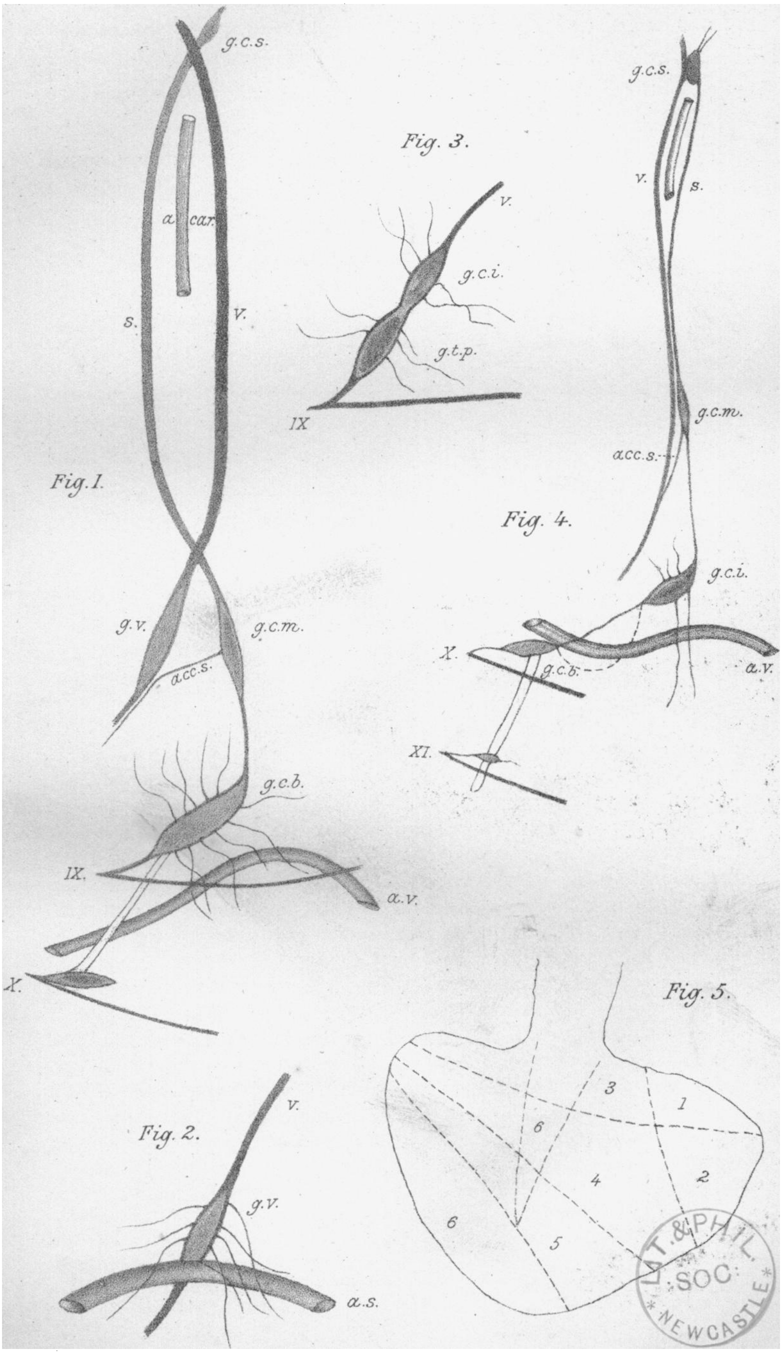
Fig. 1. Relations of the sympathetic, vagus, &c., in *Chelonia imbricata* and *C. caretta.* S., sympathetic; V., vagus; *g.c.s.*, ganglion cerv. super.; *a. car.*, arteria carotida; *g.v.*, ganglion of the vagus stem; *g. c.m.*, ganglion cerv. med.; *g.c.b.*, ganglion cardiac basal; *acc. s.*, accelerating symp. branch; *a.v.*, arteria vertebralis; ix, x, refer to the metamere concerned.

Fig. 2. The vagus ganglion with its leash of branches. *a.s.*, art. subclavia.

Fig. 3. Shows partial fusion of *g.c.i.*, the gang. cerv. infer., and *g.t.p.*, the gang. thoracic prim.

Fig. 4. The sympathetic, &c., in the *Terrapin*; to a large extent the same in *Chelonia mydas.* The lettering, as in previous figures. The dotted line between *g.c.i.* and *g.c.b.* indicates that a branch sometimes present completes an *annulus Vieussenii.*

Fig. 5. Ventricle with areas marked off by dotted lines, the numbers indicating the order in which these areas lie.



F. Huth, Lithr. Edinr.

HEART OF SEA-TURTLE.