XVIII. The Croonian Lecture.—*On the Influence exercised by the Movements of Respiration on the Circulation of the Blood.* *By* J. Burdon Sanderson, *M.D., F.R.C.P. Communicated by Dr.* Sharpey, *Sec. R.S.*

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Having in the course of an inquiry relating to the order of cessation of the vital phenomena in apnœa, the results of which I propose shortly to submit to this Society, been led to doubt the truth of the received opinion as to the influence exercised by the movements of the chest in respiration on the circulation, and having found that similar doubts were entertained by others who had given attention to the subject, I thought it necessary before proceeding further to endeavour to obtain a solution of this most important question by experiment.

Part I.—PREVIOUS RESEARCHES.

It is to Professor Ludwig that we owe the first application of exact methods in the investigation of the influence of the thoracic movements on the action of the heart. In 1846 he performed a series of experiments, the results of which were published the following year in Müller's 'Archiv'*. In these experiments he employed an instrument (called by him a Kymographion) by which the readings of a hæmadynamometer attached to an arterial trunk were inscribed on a cylinder revolving by clockwork at a uniform rate. He found that in ordinary respiration the tracing of the kymographion always exhibited characters which were distinctive, consisting of large undulations or waves produced by the thoracic movements, the contours of which were broken by smaller waves expressing the contractions of the heart. As regards the relation between the

* "Beiträge zur Kenntniss des Einflusses der Respirationsbewegungen auf den Blutlauf im Aortensysteme," Müller's Archiv, 1847, p. 242.

greater or respiratory wave and the thoracic movements, it appeared to LUDWIG that the descending limb (or to speak more shortly, the *descent*) of the wave was coincident with the expansion of the chest in inspiration, and that the ascending limb (or *ascent*) corresponded to the time occupied by the collapse of the chest in expiration and the succeeding pause, so that the summit of the wave indicated the commencement of inspiration. And with respect to the smaller or cardiac waves, he observed that in the ascent of the great wave they were more frequent and more abrupt than in the descent, whence he inferred that during expiration the contractions of the heart succeed each other with great rapidity and are separated by short periods of relaxation, whereas during inspiration the heart remains relaxed for some time between each contraction and its successor.

In most of these experiments the arterial pressure only was traced on the cylinder of the kymographion; as, however, it was found that under certain circumstances the relations between the respiratory movements and the undulations of the tracing were obscure, the experiment was modified. An elastic bag containing air was introduced into the cavity of the pleura by an aperture to which the mouth of the bag fitted air-tight. The bag was connected by a flexible tube with a second bag, the expansive movements of which were transmitted by a lever to the cylinder of the kymographion, on which a tracing was inscribed simultaneously with that which indicated the arterial pressure. It was found that the expansion of the bag connected with the pleura did not always coincide with increased arterial pressure. These inconsistencies did not, however, appear to be of such a nature as to render it necessary to abandon the theory which had been adopted. Although LUDWIG had evidently some misgivings as to its truth, he did not continue the investigation; for in a prefatory note to a paper by EINBRODT, published in 1859, LUDWIG states that during the preceding twelve years he had abandoned the inquiry although convinced that he had misunderstood the connexion of the facts*.

[*Note.*—In the last edition of his 'Lehrbuch der Physiologie,' LUDWIG gives the following account of the changes of arterial pressure consequent on the respiratory movements:—"At the beginning of expiration the contractions of the heart become more frequent, the mean tension of the blood increases, so that even during the relaxation of the heart it sinks very inconsiderably or not at all. Every new contraction induces a higher tension than its predecessor. At the close of the expiratory movement, when the narrowed thorax resumes its normal size, a long pause in the heart's action suddenly occurs, during which the tension sinks considerably, and the movements of the heart are in consequence retarded." This passage shows that until 1861 the author entertained the same views as in 1859.]

In 1860 LUDWIG's experiments were repeated by EINBRODT, who published his results

* "Ich hatte mich überzeugt dass ich in meiner früheren Arbeit die an und für sich richtigen Thatsachen nicht richtig verknüpft hatte."

in MOLESCHOTT's 'Untersuchungen'*. Of these experiments, which were performed in LUDWIG's laboratory, and apparently at his suggestion, there were two series. The first related to the effect produced by the artificial production and maintenance for various periods in the air-tubes of pressures which either exceeded or fell short of the pressure of the atmosphere by several inches of mercury. The second series, which alone directly concerns the present inquiry, consisted of experiments with the kymographion, in which either the movements of the thoracic walls or those of the respired air were recorded on the cylinder simultaneously with the variations of arterial pressure. The animals employed (dogs) and all the other conditions were the same as in the previous experiments of LUDWIG, and the difference in the mode of recording was insignificant. The arterial tracings were of the same form as those obtained by LUDWIG, but the relation of the arterial to the respiratory wave was such as to lead EINBRODT to opposite conclusions. According to EINBRODT, "the mean arterial pressure is slightly diminished at the very commencement of inspiration, but immediately afterwards gradually and constantly rises, while the action of the heart is accelerated. The pressure continues to rise until the beginning of expiration, when it reaches its maximum. Thereupon a pause is usually, but not constantly, observed in the contractions of the heart, in which of course the arterial pressure sinks considerably. It always happens that during the remainder of expiration the pressure is diminished while the action of the heart is retarded."

The only other observations by which our knowledge of this subject has been materially advanced are those of MAREY, made with the aid of the instrument invented by him, and described in his work on the Physiology of the Circulation, under the name of "Sphygmographe." By this instrument, the purpose of which is to measure the arterial tension in the living human subject and to record its rhythmical changes by mechanical means, a tracing may be obtained (provided that the individual under observation breathes largely or with effort) which exhibits characters essentially the same as those described by LUDWIG, that is to say, by taking corresponding points in a series of arterial oscillations and connecting them with each other, a curve is produced consisting of larger waves, which are in relation with the thoracic movements. MAREY found that the nature of this relation differs according as the individual breathes with widely open or partially closed respiratory apertures. When respiration is performed largely and without obstruction, the ascent of the respiratory wave coincides with inspiration, the descent with expiration; whereas when the movement of air is obstructed by the narrowing of the air-channels, and each respiration is performed with great effort though with little effect as regards the quantity of air introduced, the curve descends in inspiration, ascends in expiration. These differences MAREY thus explains: in free breathing the diaphragm presses on the aorta and thereby increases the arterial pressure. In restricted breathing the movement of the diaphragm and consequently its influence is diminished, while on the other hand those changes of tension in the thoracic cavity, which under

* "Über den Einfluss der Athembewegungen auf Herzschlag und Blutdruck," MOLESCHOTT's Untersuch. B. vii. 1860.

ordinary circumstances are very inconsiderable, are manifestly increased whenever the influx and efflux of air are obstructed*.

Part II.—EXPERIMENTS.

The inquiry was commenced in 1864 and continued at various periods during 1865 and 1866. Dogs were exclusively employed. On account of the mobility of their chests, and the great variety they exhibit in the mode of breathing, these animals are especially adapted for the purpose required. In every instance the respiratory movements and the changes of arterial pressure were recorded mechanically on paper moving horizontally by clockwork.

1. *Description of the Apparatus.*

a. *Respiratory movements.*—For the purpose of recording the respiratory movements, a disk-shaped bag of caoutchouc about 6 inches in diameter is used. In the earlier experiments the material employed was vulcanized, but subsequently non-vulcanized india-rubber was preferred. Each of the opposite sides of the bag is glued to a circular disk of wood, which being of smaller circumference leaves a free margin of half an inch round the edge. Of the two boards the lower is fixed, the upper moveable. The latter is screwed to a double horizontal arm of whalebone, the effect of which is to support it horizontally about half an inch above the level of its fellow. By means of this arrangement the expansive and vertical movements of the bag are limited in such a manner that an equal resistance is afforded by the elastic whalebone to the ingress and egress of air. The centre of the moveable disk is connected, by means of a vertical rod, with a lever of the third kind, which is made of light wood terminating in whalebone, and has a total length of 25 inches. The lever works on a steel axis fitted to it by a socket of brass; the axis is supported by a framework of brass which slides up and down on two rectangular brass rods, and is so arranged as to be readily adjusted and fixed by a screw at any desired height. The lever bears at its extremity a fine sable brush which is fixed horizontally at right angles to its length. Communication is made between the respiratory passages of the animal and the caoutchouc bag by a T-shaped tube of

* The present state of opinion on the question may be gathered from the following quotations from the most recent physiological works:—

"During expiration the external surface of the heart is subjected to a stronger pressure than during inspiration, which is expressed in the greater frequency of its pulsation and in the rise of the mercury in the dynamometer." —Budge, *Lehrbuch der spec. Physiol.* 1862, p. 350.

After referring to the most recent researches, particularly those of Marey, the editor of the last edition of Dr. Carpenter's 'Physiology' says, "During the act of expiration the frequency of the pulse is considerably augmented, whilst the line of mean pressure rapidly rises, indicating increased tension in the arterial walls. . . . . During the act of inspiration, on the contrary, the pulsation becomes slower, the curves much bolder, and the line of mean pressure gradually falls; for then the blood readily enters the thorax, and, as a consequence, the great veins, capillaries, and arterial walls become comparatively flaccid."—Carpenter's *Physiology*, last edition, 1864, p. 245.

gutta percha, one arm of which is connected with the trachea, the other with the elastic bag by a flexible tube of equal width with itself. The third arm remains open. The slight resistance afforded by this arrangement to the flow of air produces sufficient movements of the lever to indicate the exact duration and relative intensity of the respiratory movements.

b. *Variations of arterial pressure.*—As the purpose of the investigation was not to measure the absolute arterial pressure, but to determine the variations of pressure with reference to their duration and order of succession, it appeared unnecessary to employ a more complicated apparatus than the following, from the construction of which it will be seen that the results obtained by it are subject to the error due to the difference of level between the arterial aperture of the animal and the surface of the mercury at the commencement of the observation. The error in question would rarely exceed a tenth of an inch of mercury. The hæmadynamometer employed is a U-shaped tube of glass, of which the longer arm measures 15 inches, the shorter 10 inches. It differs from the hæmadynamometer of POISEUILLE in this respect, that the attached arm, which is the longer of the two, is of smaller calibre than the open arm, the area of the mercurial column contained in the latter being about twelve times as great as that in the other. Hence for every variation of an inch of pressure the surface of the mercury in the open tube moves only one-thirteenth of an inch. The movements of the mercury are transmitted to the recording cylinder, by a lever of the same length and supported on a moveable bearing in the same manner as the one described above. This lever is connected by a vertical rod of iron wire with a conical cork float which rests on the surface of the mercury contained in the wide arm, its base being concave, so as to correspond with the convexity of the meniscus. The joint by which the vertical rod is connected with the lever is so arranged that for every inch of variation in pressure a nearly vertical movement of the extremity of the lever carrying the brush, amounting to three-tenths of an inch, takes place. In order that the lever may accurately follow all the oscillations of the mercury, its dead weight is nearly neutralized by a weight of lead suspended beyond the fulcrum. A similar counterpoise is attached to the lever for recording the respiratory movements.

c. *The recording apparatus* consists of two cylinders, each of 10 inches in diameter, both of which revolve vertically. They are connected together by the band of paper on which the tracing is to be made; this band as it is delivered from the one is wound round the other. The motion of the receiving-cylinder is produced by the descent of a weight and regulated by clockwork to which the feeding-cylinder is adapted. The movements of the levers are inscribed on the paper in its transit from one cylinder to the other. The rate of movement of the paper admits of being varied according to the requirements of the experiment, but in most instances it was such that 10 inches were delivered in a minute. It is obvious that although the greatest care may be taken to adjust the levers in such a manner at the commencement of each observation that the points of the brushes are in the same vertical line, this relation can only be maintained so long as the two levers are parallel. When therefore great variations of arterial pressure take place in the course of an experiment, it is necessary in order to determine the synchronism of the events recorded, to adopt some method of marking synchronical points in the two tracings inscribed simultaneously on the paper. This object is best attained by making simultaneous momentary interruptions by withdrawing the levers from the paper at the same instant. With this view the stand on which the lever-apparatus and manometer are fixed is so constructed as to have a horizontal rotatory movement round a fixed pin, the position of which nearly coincides with the base of the rectangular brass rods on which the bearings of the levers are supported. By this movement, which is regulated by a screw, the operator can at will approximate or withdraw the points of the brushes.

2. *Experiments as to the relation between the arterial pressure and the movements of the thorax in the normal animal.*

The first experiment was made in the Museum of Middlesex Hospital on the 14th of September, 1864. The dog having been secured in the usual manner, the dynamometer was adjusted to the femoral artery, and as soon as the breathing had become tranquil, a mask of gutta percha of a suitable form was placed loosely over his snout and connected by a tube with the vulcanite bag. In this preliminary experiment it was observed that "each inspiratory descent of the lever was accompanied and followed by an arterial ascent, that is to say, by a succession of short and quick oscillations, which imply that during the period they express, the ventricles of the heart became fuller and fuller, their systole more vigorous but less complete, and their diastole accelerated; while in the interval between each inspiration and its successor the arterial pressure sank, the contractions of the ventricles were more rare, and the diastole of longer duration."

The investigation was resumed in the physiological laboratory of University College, the apparatus having been in the meantime entirely reconstructed. Preliminary experiments were made on the 2nd, 3rd, 9th, and 11th of March, which yielded results in accordance with those previously and subsequently obtained. The apparatus was not, however, brought to a satisfactory state of completeness till the end of May, after which the observations given in the Plates were made.

Observation I.—June 10th, 1865 (Plate XXIII. fig. 1).

A male terrier of moderate size was secured on its back in the usual way, viz. by ligatures attached to each extremity. The femoral artery having been exposed, a silver canula, previously filled with saturated solution of carbonate of soda, was introduced and secured. The trachea was then laid bare about 1 inch from its upper end, and partially cut across. A glass tube as large as it would admit was inserted and secured by a ligature, which was then connected with the caoutchouc bag by means of the T-shaped tube above described, while the communication between the artery and the dynamometer was completed by a vulcanite tube filled with solution of carbonate of soda*. It having been ascertained that the apparatus was in order, and the dog breathing quietly, the clockwork was set in motion, the rate of horizontal movement of the paper being 1 inch in six seconds. The tracings show that there were about nine respirations and 108 pulsations per minute. The upper or arterial tracing is crossed by a faint horizontal line, which indicates a pressure of 6·2 inches of mercury†. During the progress of the observations the brushes were simultaneously withdrawn from the paper at short intervals, so that synchronical points could be accurately taken. The tracings show that the period occupied by each respiratory act is divisible into two parts, one of which (about two-fifths of the whole) is occupied by the thoracic movements, the remainder by the pause. Of the first part, two-thirds correspond to inspiration, one-third to expiration. It is further seen that the effects of the thoracic movements are as readily discernible in the respiratory as in the arterial tracing. The part of each arterial tracing corresponding to a single respiratory interval consists, as described by LUDWIG, of a great wave, the contour of which is broken by smaller waves, each representing a contraction of the heart. During the whole period of the pause the arterial pressure gradually sinks. The commencement of inspiration is immediately followed by an increase of pressure, which becomes still more marked during expiration; but no sooner is the expiratory act completed than it again subsides. The apex of the greater or respiratory wave in the arterial tracing is therefore coincident with the end of expiration. As regards the effect of the thoracic movements on the duration of each cardiac revolution, it is no less distinctly seen that the interval between each two succeeding contractions is about three times as great in those pulsations which immediately follow the end of expiration as in those which precede it, and that this interval gradually diminishes until the next corresponding period. At one part of the tracing, where the inspiration lasted longer and was deeper than usual, it is seen that the consequent elevation of pressure and acceleration of pulse was greater‡.

Observation II.—June 16th, 1865 (Plate XXIII. fig. 2).

The animal employed was a male mongrel dog of moderate size. The experimental method was the same as before, with the exception that the rate of movement of the paper was about twice as quick. The synchronical points are marked by simultaneous interruptions, and by dots indicating the relative position of the brushes§. The faint

* In my earlier experiments, although a saturated solution was always used, the blood sometimes coagulated before the observation was completed, rendering it necessary to remove, cleanse, reinsert, and reconnect the silver canula. To prevent this result a pressure of about 5 inches of mercury, *i. e.* nearly equal to that usually existing in the arteries of a dog, was first produced in the dynamometer (by a mechanical arrangement which it is not necessary to describe) before completing the connexion. When this precaution was taken, very little blood passed beyond the silver tube in the artery, and even there was mixed with the saline solution in such proportion that no coagulation took place.

† The absolute value of this result is subject to the exception made at p. 575.

‡ This animal was afterwards employed in an experiment on asphyxia.

§ These faint horizontal lines and the dots have been omitted in the engravings.

horizontal line denotes an arterial pressure of 5 inches. The rate of breathing was 11–12 per minute, and of the heart's contractions 94. It is to be noted that in this animal the time occupied by the thoracic movements was greater as compared with the duration of the pause. Hence probably the variations of the arterial tracing are less abrupt. It is further to be noted that the diastolic interval is shortest a little after the commencement of expiration, and longest immediately after its termination*.

Observation III.—June 13th, 1865 (Plate XXIII. fig. 3).

The animal employed was a small male English terrier. Experimental method as before; rate of movement 1 inch in six seconds; arterial pressure 5 inches; eleven respirations and seventy pulsations per minute. From the relative length of the respiratory intervals and the great regularity of the arterial undulations, the precise relation between the two tracings can be determined with great exactitude.

Observation IV.—May 31st, 1865 (Plate XXIII. fig. 4).

Animal used, a smooth black male English terrier. In this case a T tube with a very wide aperture was employed; hence the oscillations of the lever were so slight that the commencement of inspiration cannot be distinguished. The moment at which the expiratory act commences and terminates is, however, clearly indicated. Rate of movement 1 inch in 3·3 seconds; arterial pressure 5 inches; the respirations were more frequent than in any of the previous cases, being 32 per minute; as there were 100 pulsations in the same time, three occurred during each respiratory act. Notwithstanding this peculiarity the relation between the two remained the same; the highest points in the arterial tracing corresponding to the end of expiration, and the diastolic interval immediately after that event being twice as long as the one preceding it†.

Observation V.—June 21st, 1865 (Plate XXIII. fig. 5).

A male mongrel terrier of good size was employed. Arterial pressure 6 inches (indicated by horizontal line); rate of movement 1 inch in three seconds; respirations 16, pulsations 102 per minute. The tracings exhibit the following peculiarities:—the respiratory movements were more irregular, and the time occupied by them was greater as compared with the pause; so much so that it several times happened that there was no interval at all between expiration and inspiration. The effects of this mode of breathing are well seen in one part of the tracing, where two inspiratory descents succeed each other almost immediately, in consequence of which a high arterial pressure is maintained for several seconds. The irregularities of the respiratory tracing are, so to speak, reflected in the arterial, each respiratory undulation having the same duration as the arterial undulation which corresponds to it‡.

* The animal was used for other experimental purposes.

† The animal was further used for an experiment relating to the poisonous effects of carbonic acid.

‡ This animal was subsequently used in an experiment on poisoning by hydrocyanic acid.

Observation VI.—May 30th, 1865.

The animal used was a large-sized male mongrel terrier. Rate of movement 1 inch in 3·3 seconds; arterial pressure 5 inches; respirations seventeen, pulsations seventy-six per minute. From the irregularity of the respiratory movements it is more difficult to make out the relation between the two tracings, which, however, is in conformity with previous observations. Those inspirations which were deepest and longest produced the most marked effect*.

Observation VII.—June 20th, 1865.

The animal used was of the same description as in the last experiment. Rate of movement 1 inch in 3·3 seconds; arterial pressure 5 inches; respirations twenty to twenty-two, pulsations sixty per minute. In this animal the variations of arterial pressure were very slight; but as regards the diastolic intervals the facts of previous observations were confirmed†.

Observation VIII.—June 17th, 1865.

A female mongrel cur of moderate size was employed. Rate of movement 1 inch in three seconds; arterial pressure 5 inches; twenty-one respirations and fifty-eight pulsations per minute. In this animal the respiratory movements were unusually frequent as compared with the contractions of the heart. Occasionally the cardiac and respiratory intervals are shown in the tracings to be nearly equal, in which case it is obvious that the thoracic movements could not produce any effect on the variations of arterial pressure. If, however, the respiration was retarded, the usual variations manifested themselves, as is well seen in the second part of the tracing, where the frequency of the pulse happens to be twice as great as that of the breathing. The diastolic interval which follows inspiration is here found to be not more than half the length of that which coincides with it. Again, towards the end of the observation, where the animal is seen to have sighed deeply, a succession of short diastolic intervals with increasing arterial pressure is seen to follow the expansion of the chest, and to be of corresponding duration‡.

Observation IX.—June 24th, 1865.

A male cur was employed in this experiment. Rate of movement 1 inch in three seconds; arterial pressure 5 inches; respirations nineteen, pulsations ninety-six per minute. The influence of the thoracic movements on the arterial pressure was not marked, excepting when the inspirations were deeper than usual. It is worthy of notice that there was a distinct pause between inspiration and expiration, as illustrated in the first part of the tracing, which serves to show that the expiratory act, unless it is unnaturally forcible, is without effect on the arterial pressure§.

* The animal was further used for other experimental purposes.

† The animal was subsequently used in an experiment as to the toxic effects of hydrocyanic acid.

‡ This animal was further used for an experiment as to the influence of strychnia on the thoracic movements.

§ The animal was subsequently employed for an experiment as to the toxic effects of hydrocyanic acid.

Observation X.—June 28th, 1865.

A full-sized male mongrel. Rate of movement 1 inch in six seconds. The animal struggled excessively on being secured, and breathed during the period of observation 120 times in a minute; the frequency of the heart's action being from 190 to 200. The respiration was occasionally interrupted by deep sighs, the effect of which on the arterial pressure is well shown in the tracing. Each sigh was accompanied by an immediate and rapid increase of pressure, which was followed by a corresponding acceleration of the action of the heart*.

Observation XI.—August 9th, 1865 (Plate XXIII. fig. 6).

A male English terrier was employed in this experiment. The trachea was not opened, the communication between the air-passages and the caoutchouc bag being effected by means of a moist bladder tied over the snout. The mouth of the bladder was adapted to the T tube already described. In order to ensure the animal's breathing freely, the teeth were kept apart by a wooden wedge. Rate of movement 1 inch in three seconds; respirations eighteen, pulsations sixty-four per minute. The observation illustrates the effect of a mode of breathing which, although not strictly normal, is frequently seen in the dog. The animal inspired suddenly, the time between each inspiration and its successor being for the most part occupied by a prolonged whine terminating in a short expulsive movement which was immediately succeeded by inspiration. During the whine the respiratory lever remained at the same level or ascended very gradually. As regards the arterial pressure, the tracing shows that in this instance the rapid rise of the mercurial column coincided with the commencement of the whine, and that it began to fall one or two seconds before inspiration, so that the period of decline corresponded to the last half of the period of expiration and to the whole of the period of inspiration.

The preceding observations afford conclusive evidence that in dogs the expiratory act is not the cause of the elevation of the arterial pressure which is associated with each respiration, for they show that the elevation invariably commences and is sometimes at an end before inspiration is completed. It can therefore scarcely be doubted that the effect in question is due to the expansion of the chest; for if not caused by expiration, there is no other possible agency to which it could be attributed. It is now necessary to show that the conditions of experiment, in so far as they were unnatural, were not such as to interfere with the natural performance of the respiratory function, and that whatever explanation is applicable to the phenomena recorded, must necessarily be equally applicable to ordinary breathing in the dog.

The mode in which the animals were secured, and the contrivances employed for transferring to paper the movements of the air in and out of the respiratory cavity, have been already described. It might be objected that the natural breathing would be interfered with, either by the pain and terror of the operation, by the absence of the controlling influence of the larynx, or by the resistance offered to the influx and efflux of air in its

* The animal was afterwards used for an experiment on carbonic oxide.

passage through the breathing-tube. The first of these objections is, I think, answered by the tracings. It is seen that in almost every instance they were performed with perfect regularity, and that in several they were remarkably slow as compared with the ordinary rate of breathing in the dog. Although no anæsthetic was used, yet from the simplicity of the operations performed and the rapidity with which they were completed, the animals were in a perfectly tranquil condition during the periods of observation. Importance is also to be attached to the circumstance that dogs of impure breed were always employed. The second objection is of little value; for it is well known that in the tranquil breathing the rhythmical laryngeal movements have no appreciable influence on those of the thorax. But the third is of sufficient weight to demand not only consideration but special inquiry.

In preliminary experiments I found that when the caoutchouc bag was connected with a mask placed loosely over the animal's snout, the movements communicated to the lever were of the same nature as those represented in the tracings, although of greater extent. I had also repeatedly found that the apparatus was so sensible that if the aperture of the T tube was placed opposite the nostril at an inch distance, the opposite aperture being closed, movements of the lever were produced by the air passing in and out in ordinary breathing. By these facts, as well as by the comparison of the width of the T tube with that of the natural air-passages, I was convinced that, so far from the resistance afforded being greater, it was considerably less than in ordinary breathing through the nostrils. Further, from what I believed I had ascertained as to the mode in which the results are produced, I was led to expect that they would not have been in the slightest degree modified even if the resistance had been many times as great as it actually was. For the purpose of testing the truth of this assumption I made the following experiment.

Observation XII.—June 15th, 1866 (Plate XXIV. figs. 1–4).

A male brindled mongrel terrier, weighing 30 lbs., was employed. 3·1 cubic centimetres of a solution of hydrochlorate of morphia, containing one grain per cubic centimetre, was injected into the cellular tissue of the axilla. The animal became torpid almost immediately; there were no convulsions. The usual operation was then performed. The connexions having been completed, the clockwork was set in motion twenty minutes after the injection of the morphia; the rate of movement of the paper being 1 inch in 2·9 seconds, and the arterial pressure 5 inches. Observations were continued for an hour, during the whole of which period the breathing was regular. The T tube which was employed had an internal diameter of four-tenths of an inch; and in order to produce various degrees of resistance cylindrical corks were used, the transverse sections of which were reduced by slicing them in planes parallel to their axes, but at various distances therefrom. Thus, between the cork and the tube containing it, an air-passage was left, of which the section was an arc of a circle of four-tenths of an inch in diameter. The corks so prepared were severally marked A, B, C, and D. The form of the section of the cork used in the production of each tracing is shown in the

1 (fig. 1). Cork B was inserted in the tube, but by inadvertence a second aperture in the caoutchouc bag intended for a different purpose was left open. As it was of equal diameter with the tube by which the bag is connected with the trachea, the resistance offered by the apparatus in this instance was extremely small. This is indicated by the inconsiderable extent of the oscillations of the respiratory lever. Measurements show that the acceleration of the contractions of the heart, and the increase of arterial pressure, occurred invariably two-thirds of a second after the commencement of each inspiration.

2 (not engraved). Cork B was again used, but the second opening in the caoutchouc bag was closed. The increased resistance is denoted by the depth of the inspiratory descent. The characters of the arterial tracing remain unaltered. It is to be observed that whenever inspiration was performed with greater suddenness than usual, its influence on the arterial tracing was more transitory, and the interval between the inspiratory act and its effect was shorter.

3 (fig. 2). Cork C was employed. The extent of movement of the lever was much increased, but the characters of the arterial tracing are the same.

4 (fig. 3). By inserting the cork D, which almost filled the aperture of the ⊤ tube, the resistance was increased to the utmost. The main features of the arterial tracing are unchanged, but the variations of arterial pressure occur at a shorter interval, viz. four-tenths of a second after the thoracic movements. The breathing was slightly accelerated, the number of respirations per minute being thirteen as compared with eleven at the beginning of the period of observation.

5 (not engraved). The cork A was substituted for D. The breathing appeared to be perfectly free, the extent of movement of the lever being scarcely greater than when the aperture was left entirely open.

6 (not engraved). Soon after the last observation, viz. an hour and five minutes after the commencement of the experiment, the breathing became irregular, the respiratory movements becoming unequal both in duration and depth, although no change was made in the apparatus. The effects of these variations are seen in the tracing.

7 (fig. 4). In order to carry the investigation one step further the open arm of the ⊤ tube was completely closed, so that the limited quantity of air contained in the connecting tube and in the caoutchouc bag was repeatedly respired. The tracing was made during a period commencing twenty-three seconds after this had been done, and shows that the movements of the respiratory lever were still more ample, and particularly that the inspiratory efforts were so energetic that the caoutchouc bag was emptied each time the chest expanded. This is indicated by the horizontal line between the descending and ascending limb of the curve. The breathing was scarcely at all accelerated (12–14 per minute), and the arterial tracing retains the same character as before. The increased arterial tension and acceleration of the pulse lasted in each case during the whole of the period of inspiration.

The series of results just stated afford evidence that the relation previously observed between the thoracic movements and those of the heart do not depend on mechanical conditions peculiar to the mode of experiment; and they furnish additional proof that it is not affected by the abnormal psychical conditions of the animal, which in this instance was throughout under the influence of morphia. It may therefore be assumed that in the dog, so long as the respiratory passage is sufficiently open to allow of the entrance of air into the chest, the act of inspiration is invariably followed in normal breathing by increase of tension and shortening of the diastolic interval, *i. e.* acceleration of the heart's action*. It remains to be considered by what instrumentality this influence is exercised. The facts indicate that the result consists in an alteration of the mode of contraction of the heart. That part therefore of the nervous system which presides over the movements of that organ must be concerned in its production. But the effect may be brought about either by agencies which are entirely mechanical, *i. e.* altered relations between the pressures existing in different parts of the circulation, or may be also more or less due to changes in the chemical state of the circulating fluid. For this reason the proper course seems to be, first to determine to what extent the increased activity of the heart which follows each inspiration may be accounted for as a mechanical effect of the expansion of the chest. Then, even if it be found that the whole of the observed phenomena may be thus explained, it will still be open to question how far the chemical consequences of each respiration may be also concerned in their production.

The effect of the respiratory movements on the arterial pressure stands in relation to the fact, demonstrated by DONDERS, that all the organs contained in the chest are kept when its walls are at rest (as *e. g.* after death) in a state of distension, so that the mass of the thoracic viscera has constantly a tendency to shrink to a smaller volume than that of the cavity in which they are contained. As all of these organs possess elasticity, they must necessarily all participate in any expansion of the whole mass, but inasmuch as they resist expansion in very different degrees, their participation is unequal. Of the four principal kinds of organs contained in the chest, viz. the lungs, veins, arteries, and heart, the arteries and heart (when contracted) are by far least capable of distension, for they are already distended by an internal pressure equal to that of 5 to 7 inches of mercury. Consequently in inspiration the arteries and contracting heart take little or no part in the amplification of the chest; so that the increase of bulk produced by dilatation of the thorax is for the most part divided between the lungs, the great veins, and the heart when in a state of relaxation. The actual ratio between the resistance to expansion of the arteries and that of the veins may be inferred, from what we know of the relative tension of the blood in the two systems of vessels, to be about 20:1.

In ordinary inspiration with free access of air two effects are produced. The tension of the air contained in the respiratory cavity is reduced, and the resistance to expansion of the lung is increased. These two conditions exercise a similar influence on the

* If, however, the communication between the chest and the atmosphere is completely closed, the relation is reversed. The variations of blood-pressure in the arteries then become coincident in time and of similar extent with those of air-pressure in the thoracic cavity. This will be shown in my paper on apnœa.

thoracic veins and heart. The former, however, is of little importance, for its operation is inconsiderable in itself, and is moreover confined to the period during which the thorax is actually expanding. It is to the latter condition (the resistance offered by the contractility of the lung to expansion) that the effect of inspiration is mainly referable. If the veins, like the lungs, contained air, and communicated freely with the atmosphere, they would evidently expand as rapidly. Actually their expansion is much slower, so that during the act of inspiration the relation between their expansibility and that of the lung is altered, the *proportion* of the thoracic space occupied by the lungs being increased, that occupied by the veins being diminished. Correspondingly the resistance to dilatation of the lungs, as compared with the resistance offered by the mass of intrathoracic organs, is increased, that of the veins diminished. If the chest continues expanded the balance between the two resistances is gradually restored, that is to say, the veins fill with blood until their distension attains the same proportion to that of the lungs which it possessed before inspiration. Hence it follows that the repletion of the veins produced by inspiration varies in degree according to the length of the period during which the expansion of the chest continues, so that by a short inspiration, however deep it may be, scarcely any effect will be produced on the circulation. As during diastole the cavities of the heart are affected by the movements of the thorax, in precisely the same manner and probably in about the same degree, the preceding considerations are as applicable to them as to the veins, *mutatis mutandis.*

In expiration a slight increase of tension of the air contained in the air-passages takes place. But if the efflux of air is free and unrestrained, this influence is so inconsiderable as to be without influence on the thoracic organs. The only way in which expiration can materially affect the circulation is by diminishing the capacity of the thorax. In *regular* breathing its effect must be always equal to that of inspiration; for whatever increase of the calibre of the veins results from the expansion of the chest, must be reduced when it collapses.

But if in any expiratory act more air is expelled by the forcible contraction of the expiratory muscles than has previously been inhaled, the capacity of the veins will be thereby reduced in a degree proportional to the diminution of the capacity of the chest itself. Thus, if it were possible for the chest to be so contracted by the action of the expiratory muscles as to allow the lungs to collapse to a bulk equal to that which they assume when left to themselves, their tendency to contract would be in abeyance and their distending influence on other organs contained in the chest would no longer be exercised. Similarly, in all less degrees of contraction, the distension of these organs must be proportionably diminished. In other words, *the difference between the pressure to which the thoracic veins are exposed and that of the atmosphere* (the so-called negative pressure), *varies with the volume of the thoracic cavity provided that the air-passages are open.*

The preceding considerations lead to the conclusion that the dilatation of the chest in inspiration aids the expansion of the heart during the diastole, and of the thoracic veins.

The explanation cannot, however, be regarded as complete unless reference is made to other conditions not yet taken into account, *i. e.* to variations of the velocity of the circulation, and of the pressure existing in the systemic veins. For although there can be no doubt as to the *direction* in which increase or diminution of the external pressure to which the thoracic veins are exposed must affect the quantity of blood which they convey to the heart, the *degree* in which their influence is exercised must depend on the fulness of the veins outside of the chest. In healthy animals these two conditions are inseparably associated together. The more rapid the circulation, the fuller are the veins as compared with the arteries. When the veins are distended and the movement of the blood is rapid, the filling of the cavities of the heart, in diastole, takes place in a shorter period, while at the same time the contraction of both auricle and ventricle is more sudden and effective in consequence of the diminished arterial resistance. In the opposite case, when the veins are empty and the movement of the blood within them is sluggish, the cavities of the heart fill slowly, and empty themselves imperfectly in consequence of the excessive arterial resistance.

This being admitted, it may be readily understood that the effect of inspiration is likely to be materially influenced by the relative velocity and tension of the arterial and venous circulations. In the one case the right auricle, at the moment of commencing diastole, is still full of blood (*i. e.* when the arterial tension is high, the veins empty and the circulation retarded), in the other the right auricle is empty at the end of systole. In other words, when the thoracic veins are almost emptied by the heart, at each contraction the effect of thoracic expansion is far greater than when the intrathoracic veins, even in their emptiest condition, are much fuller than those that lie outside of the chest.

It being admitted that the expansion of the chest not only aids the filling of the heart during diastole, but affords it an abundant supply of blood, the shortening of the diastolic period, and the increase of arterial tension may be readily understood. Inasmuch as the heart possesses the property of contracting the instant that its walls are dilated with blood to the proper degree, it is manifest that the more rapidly the heart fills the shorter must be its interval of relaxation, and the more frequent its contractions. It is no less obvious that increased pressure must be produced by the same agency; for, provided that the ventricles are well filled with blood at the moment that each systole commences, the more frequently they contract the greater will be the quantity of blood forced into the systemic arteries, and hence the higher will be the arterial tension.

I venture to think that the explanation I have offered of the phenomena observed is complete and satisfactory, and that it will be found to be consistent with all that has been previously ascertained. But I do not deem it the less necessary to pursue the investigation further, for by so doing I shall certainly strengthen the basis on which my theory is founded, and anticipate objections which might otherwise be made to it. Admitting, then, that the influence of the respiratory movements on the heart is partly mechanical, I proceed to inquire whether it is not also partly chemical. This may be tested by observing the results obtained when a mode of breathing is induced in which the mechanism is reversed or altered while the chemical changes are the same. For this purpose I have availed myself of the well-known properties of woorara, under the influence of which the respiratory movements cease, while those of the heart remain unaltered.

3. *Experiments as to the relation between the arterial pressure and the thoracic movements in artificial respiration.*

Observations XIII.–XVI.—August 11th and 16th, 1865, and June 2nd and 8th, 1866 (Plates XXIV. & XXV.).

The animals employed on these occasions were (1) a short-legged spotted cur, (2) a small English terrier, (3) a bull terrier weighing 13 lbs., (4) a black and tan terrier weighing $18\frac{1}{2}$ lbs. All were males. With the exception that in the last experiment the pneumogastric nerves were divided, the procedure was the same in each case. The rates of movement of the paper were as follows:—August 11th, 1 inch in 3·2 seconds; August 16th, 1 inch in 3·5 seconds; June 2nd and 8th, 1 inch in 2·8 seconds. The solution of woorara employed in 1865 was kindly given by Professor HARLEY; that used in 1866 was obtained some years ago from Professor PÉLOUZE, and is believed to have been derived from the same source as that used by BERNARD in his investigations of the toxic properties of woorara. The solution contains 0·01 gramme of the substance in each cubic centimetre. The solution was always injected into the subcutaneous cellular tissue. In the two more recent experiments the quantity used corresponded to one-tenth of a gramme of solid woorara. The respiratory movements ceased at periods varying from twelve to fifteen minutes after the injection.

The apparatus was modified so as to admit of artificial respiration. For this purpose a common pair of bellows was employed, which could be adapted at will to the open end of the ⊤ tube. The caoutchouc bag was provided with a second tube of the same size as that by which it was connected with the ⊤ tube. This additional tube was kept closed so long as the animal continued to respire naturally. As soon as it was desired to practise artifical respiration, air was injected by the bellows; of this air a sufficient proportion inflated the chest, while the remainder passed out through the caoutchouc bag. Immediately after each stroke of the bellows the air introduced was expelled by the elastic reaction of the thoracic walls. By this arrangement the too forcible inflation of the lungs was effectually prevented, and the complete removal of breathed air from the apparatus was ensured. As the experiments were all of the same nature, I prefer to enumerate the results obtained rather in their relation to each other than in the order of time.

1. Under certain circumstances, and particularly when artificial respiration is practised at long intervals, the inflation of the lungs appears to produce analogous effects to those of ordinary breathing. This was well seen during the observations made on the 16th

of August, when immediately after the thoracic movements had ceased, air was injected for some time at regular intervals, at first of ten seconds, and subsequently of fifteen seconds. In both cases each inflation was followed by an increase of arterial tension, and an acceleration of the pulse. The result of one of these experiments is shown in Plate XXIV. fig. 6, the interval between each inflation and its successor being fifteen seconds.

2. It soon, however, appeared that the relation observed on this occasion was not constant; for even in the same animal it was subsequently found that it could no longer be traced when the interval was shortened to five seconds; the variations of arterial pressure and of pulse-frequency in this case resembled those previously seen, but it was only every third stroke of the bellows that appeared to be effectual (see Plate XXV. fig. 4). A similar effect had been previously observed in the experiment of the 11th of August. Again, it was repeatedly noticed that even when artificial respiration was entirely discontinued, rhythmical variations in the force and frequency of the heart's action manifested themselves. This is well seen in Plate XXV. fig. 3, taken about an hour after the solution had been injected. Similar undulations were observed during apnœa in all the animals experimented upon, the intervals varying from five to fifteen seconds.

3. The results stated in the preceding paragraphs seem to show (1) that there is a marked tendency to periodical variations in the activity of the heart of animals under the influence of woorara, and (2) that these variations are for the most part independent of external agencies; and it seems not improbable that the apparent relation observed between the artificial thoracic movements and the fluctuations of the mercurial column in certain cases, may be due to the mechanical stimulation of the heart by the sudden inflation of the chest. However this may be, subsequent observations show that a much more marked and constant influence is exercised by the injection of air into the chest under other circumstances. In my experiment of June 2nd artificial respiration was commenced about a minute and a half after the natural breathing had ceased, and the inflations were continued at intervals of ten seconds, just as in the experiment of the previous year. About five seconds after each stroke, as is well seen in the tracing (Plate XXIV. fig. 5), the arterial pressure rose. Here the length of the interval between the two events at once suggested that the relation between them could not possibly be mechanical.

4. In other observations which were made after several minutes' discontinuance of artificial respiration this was still more evident. In all the animals I found that the heart was much less affected by the privation of air than in the normal state. Thus the inflations could be suspended for three or four minutes without making any material alteration in the character of the oscillations of the mercurial column; but when apnœa was still further prolonged the arterial pressure gradually subsided from 5 or 6 inches to 2 or 3. If under these circumstances air was injected no immediate effect was produced, excepting a slight elevation of the arterial lever simultaneous with the inflation. After the expiration of six or seven seconds the pressure began to rise, while the heart's

contractions became more frequent. This effect usually lasted for several seconds, during which the mercurial column attained an elevation which sometimes equalled and sometimes exceeded that which existed before apnœa was produced; in the latter case it soon relapsed to the normal level. Observations of this nature were made on each occasion. The tracing on Plate XXV. fig. 5 was obtained on the 8th of June. After about three minutes of apnœa, a slight inflation was made, twenty-two minutes having elapsed since the injection of the solution. The arterial pressure had sunk from 5 inches to 3. The interval between inflation and its effect was six seconds. The increased action of the heart lasted fourteen seconds, after which the mercury subsided to its former level. Again, on the 2nd of June (Plate XXV. fig. 6), twelve minutes after the injection of woorara, artificial respiration was discontinued for four minutes, at the end of which time the arterial pressure had sunk to 3 inches. The effect followed the cause at an interval of seven seconds, and lasted for about ten seconds. About half a minute after, the clockwork was stopped, and the animal was again deprived of air for four minutes. The pressure having again sunk to 3 inches, the inflation was repeated with a perfectly similar result. An observation of the same nature was made in 1865. Apnœa had existed for four minutes, the injection of woorara having been made one hour and ten minutes previously. The usual mechanical effect accompanied the inflation of the chest, but no more permanent elevation of arterial pressure occurred until about eight seconds later. It is to be noted that the effects described above could only be obtained when the arterial pressure had been considerably reduced by apnœa; for if the inflation of the chest had been discontinued for shorter periods no material increase of tension was produced by resuming it.

5. As in all the observations recorded in the preceding paragraph the interval between each inflation and its effect was too long to admit of any mechanical explanation, the phenomenon can only be referred to the chemical action of the injected air on the circulating blood. To test this I repeated the experiment on two occasions, with this difference, that hydrogen was substituted for air. In each case the result was the same. An observation of this nature was recorded on the 2nd of June; artificial respiration had been suspended until the arterial pressure had sunk to 3·4 inches. The chest was then fully inflated with hydrogen, when it was observed that the mercury, instead of rising at the sixth or seventh second, remained at the same level. Fourteen seconds after, a very slight injection of air was made, which was followed by the usual result. Still later the lungs were fully inflated with air, in consequence of which the pressure rose to 6 inches.

6. It is obvious that if artificial respiration exercises any mechanical effect at all on the circulation, that effect must be not only different from that produced by the natural movements, but of an opposite nature. For when air is injected it is evident that the expansion of the thoracic veins must be diminished, just as it is increased by natural inspiration. I have had several opportunities of observing that this is actually the case; *i. e.* that the invariable effect of inflation is to induce an immediate but very slight

increase of pressure. Thus towards the close of my first experiment, August 11th, when the animal had been for a long time under the influence of the poison, and the pulse had increased in frequency, it was found that if artificial respiration was vigorously performed at regular intervals, a tracing could be obtained of the character shown in Plate XXV. fig. 1, in which it is seen that each injection of air is accompanied by a simultaneous but very slight elevation of the arterial lever, which, however, was not associated with acceleration of the heart's contractions. This experiment was repeated under similar conditions on the 8th of June, when a corresponding but not so marked mechanical effect was observed. Ten minutes afterwards both pneumogastrics were divided in the neck. The arterial pressure at once rose to 9 inches, and the pulse attained a frequency of 240 per minute. The mercurial column remained at the same height for several minutes, during which the tracing (Plate XXV. fig. 2) was taken. Here, as in fig. 1, it is seen that the diminution of arterial pressure produced by each inflation is not accompanied with any acceleration of the heart's contractions*.

The facts related in the preceding paragraphs afford no answer to the question whether the phenomena observed are due to the direct influence of aërated blood on the heart itself, or to its indirect influence through the nervous centres over the rhythmical movements of the heart. Their principal significance in relation to the present inquiry consists in their affording ground for the inference that, whereas the effects of the thoracic movements in ordinary inspiration are almost immediate, a considerable time is required for the production of those which are due to chemical changes in the circulating blood.

4. *Experiments as to the relation between the arterial pressure and the thoracic movements after section of the pneumogastric nerves.*

It is the opinion of LUDWIG (Lehrbuch der Physiologie des Menschen, Bd. ii. p. 163) that the increased frequency of the contractions of the heart which follows ordinary inspiration is in part owing to excitation of the pneumogastric nerves. This view he supports on the ground that, although an increase of arterial tension corresponding exactly to the increased expansion of the thorax is observed to accompany the expiratory act in animals in which the vagus has been divided on each side, this effect is not associated with any acceleration of the pulse. I have already endeavoured to show that the ordinary respiratory variations of frequency of the heart's action admit of a more simple explanation; it is, however, not the less necessary to investigate the facts in question, which certainly at first sight seem to suggest such an inference as that drawn from them by LUDWIG.

It is well known that the immediate effect of section of the vagi in the neck is to diminish the frequency of respiration, and to accelerate the contractions of the heart. There are, however, several points relating to these changes which must be referred to here in their bearing on our present inquiry. The mode of respiration, after section, is

* From the extreme frequency of the contractions of the heart the oscillations of the arterial lever are not distinguishable in the engraving, although they are well defined in the original.

peculiar. Thus if you watch the movements of the thorax, you observe, first, that the chest is unnaturally dilated, and secondly, that in inspiration its further dilatation is performed slowly and with effort, and is immediately followed by an expiratory movement of so sudden and violent a character, that it resembles the collapse of an elastic bag or bladder distended with gas which takes place when its stopcock is opened. The inspiratory act, on the other hand, is not only slow but comparatively fruitless; for although the animal breathes so much less frequently than before, the quantity of air taken in at each expiration is scarcely, if at all, increased*. As regards the action of the heart, it does not appear to have been noticed by physiologists that the acceleration is not the only result produced; along with the increased frequency there is a great increase of the arterial pressure, amounting in some instances to 2 or 3 inches. This effect, although it occurs immediately after the operation, is a continuous one, and may be observed at any time after its completion.

The experiments on which these statements are founded were made at various periods during the last two years. I submit the tracings of two observations, made severally on the 29th of July and the 1st of August, 1865.

Observation XVII.—July 29th (Tracings not engraved).

The animal employed was a large, rough, mongrel terrier (male). The rate of movement of the paper was 1 inch in 7·4 seconds. The experimental procedure was the same as usual, with the exception that the two pneumogastrics were exposed low in the neck, and ligatures passed round each of them. Immediately before dividing the nerves the animal was breathing tolerably regularly fifteen times per minute, the arterial pressure being 5 inches and the rate of the pulse seventy-eight. Six seconds elapsed between the sections of the two nerves. After the division the respiratory movements became irregular and then excessive, the arterial pressure increasing at once to 6·2 inches. In less than half a minute after the first nerve was divided the breathing had again become regular, but had diminished in frequency to nine per minute, and had assumed the character usually observed after section. So long as the respiratory movements were regularly performed the mean arterial pressure remained unaltered, the variations during each respiratory act being as follows:—the highest point coincided with the end of expiration; the pressure then sank during a period of about four-thirds of a second, then gradually rose until the commencement of the next expiratory act, which was accompanied by a much more decisive increase of arterial tension, lasting for about two-thirds of a second. Immediately after section of the first nerve the frequency of the pulse increased to 150, and subsequently to 165, which latter rate was maintained. After a time the respiratory movements became irregular, occasionally, however, resuming their original character. The irregularity principally consisted in the increased extent and frequency of the inspiratory movements, in consequence of which the arterial pres-

* This statement is founded on the observations of ROSENTHAL, "Die Athembewegungen und ihrer Beziehungen zum Nervus Vagus," p. 109 *et seq.*

sure was repeatedly reduced below the original level, rising again as soon as the former method of breathing was resumed.

Observation XVIII.—August 1st (Tracings not engraved).

On this occasion a rough mongrel terrier was used. Rate of movement 1 inch in 7·1 seconds. Before section the animal was breathing somewhat irregularly, twenty-seven times in a minute, the rate of pulsation being forty-four, and the height of the mercurial column being 5 inches; twenty-three seconds elapsed between the section of the two nerves. During this interval the respiratory movements gradually increased in extent and became irregular; but immediately after the second nerve was divided the thoracic movements became so violent as to shake the table and apparatus, while the arterial pressure rose to 8 inches, remaining at that height for several minutes. The animal continued to breathe violently for about sixty seconds, during which period about twenty inhalations took place. After this the respiration assumed a more regular character, its rate varying from five to six per minute. After the first section the pulse gradually increased in frequency, finally attaining a rate of 120 per minute. This rate was maintained for two minutes and a half, when it suddenly diminished to fifty.

In all the animals I have observed after section of the pneumogastrics I have found (1) that the arterial pressure tends to increase during the slow inspiration, and to decline during the pause; (2) that a more rapid increase of tension occurs simultaneously with expiration; and (3) that this last effect, as I have ascertained by repeated measurements, never lasts for more than a second. In order to arrive at a satisfactory explanation of these facts, it is necessary to consider what is the condition of the heart and circulation after section of the vagi. The arterial tracings obtained indicate extreme abbreviation of the diastolic period combined with high arterial tension. The contractions of the heart follow each other so rapidly that the organ is in a state of continuous thrill, while at the same time they are sufficiently vigorous to maintain an arterial pressure several inches higher than the normal. In other words, the heart, although it relaxes between each contraction and its successor, never has time to empty itself, so that the whole systemic circulation is unduly distended. All this is sufficiently explained if we assume that after section of the pneumogastrics the action of the heart is intensified, the effect being altogether analogous to that which results from the injection of air into the lungs of a partially asphyxiated animal (see Observations XIII.–XVI.). It is to be further noticed that the thoracic cavity is also in a state of permanent distension, in consequence of the excessive action of the inspiratory muscles—that is to say the thoracic walls during more than half of the respiratory act remain expanded to such a degree that their elasticity is more than counterbalanced by that of the lungs.

This being understood, it appears that there are two distinct reasons why the effect of inspiration is less marked after section of the vagi than in the normal animal. It is so, first, because the diastolic period is already so abbreviated that there is no room for further abbreviation; and secondly, because the veins of the chest being already expanded beyond their normal capacity admit of no further amplification. On the other hand, the marked rise of pressure which accompanies expiration, is no doubt, as LUDWIG says, due to the compression of the air contained in the air-passages produced by the sudden contraction of the chest. It resembles the elevation of arterial pressure, which has been already described as the immediate mechanical result of sudden inflation of the lungs. Similar effects always accompany violent expiratory movements.

Conclusions.

1. The force and frequency of the contractions of the heart may be influenced either by variations in the intrathoracic pressure—viz. the pressure to which its own surface or that of the intrathoracic blood-vessels is exposed—or by variations in the chemical state of the circulating blood.

2. In natural breathing the influence exercised on the heart by each expansion of the chest is entirely mechanical. This may be inferred from its being no longer observed when the mechanism is altered, as in artificial respiration, as well as from the shortness of the interval by which the effect is separated from the cause.

[This conclusion is strongly confirmed by observations which I have made in the course of my experiments on apnœa, in which it was found that in animals asphyxiated by the continued inhalation of a limited quantity of air from a bladder, the normal relation between the thoracic movements and the arterial pressure and frequency of the pulse remains unaltered.]

3. The degree in which this influence is exercised varies according to the state of the circulation. It is greatest when the systemic veins are full, the circulation rapid, and the arterial pressure low. Under the opposite conditions it can scarcely be recognized.

4. In tranquil breathing the influence exercised by variations of air-pressure in the bronchial tubes and vesicles of the lung (amounting to about $0''\cdot02$ of mercury) (DONDERS) is so slight as to be inappreciable; and even when the extent of variation is much increased by narrowing the aperture through which air passes in and out of the chest (as in the experiments related in Observation XII.), no effect is observed which can be attributed to the impeded influx and efflux of air.

5. In forcible breathing the effects of variations of air-pressure may be recognized. This is particularly the case as regards violent expulsive movements; for whereas the effect of normal expiration is not appreciable, violent expiration is always accompanied by a simultaneous increase of arterial pressure, as *e.g.* in animals in which the vagi have been divided. In this case the elastic contractility of the lung being expended in ext pelling the air contained in the chest, the negative pressure on the external surface of the great arteries is correspondingly diminished, and hence the positive pressure against their internal surfaces is increased.

6. The increased action of the heart which results from chemical changes produced in the circulating fluid by exposure to air resembles the mechanical effect of inspiration; both being indicated by increase of arterial tension and acceleration of the pulse. The

former may, however, be distinguished from the latter, first, by the length of the interval which elapses after the introduction of air before the effect manifests itself; and secondly, by the circumstance that it is not produced at all unless the animal has been for some time deprived of air, so as to weaken the action of the heart and diminish the arterial pressure by several inches.

Finally, the relation between the respiratory movements, the arterial pressure, and the frequency of the contractions of the heart, in the dog, has been shown to be the opposite of that hitherto supposed to exist. Inasmuch as many of the conditions on which this relation depends are not the same in animals of different species, the relation itself is no doubt subject to corresponding modifications; but it may be assumed that in all animals having hearts of the same structure, variations in the quantity of blood contained in the venæ cavæ influence the mode of contraction of the ventricles, and consequently the arterial tension, in the same way as in the dog.

Note.—Professor VALENTIN, of Berne, in his recently published work (Versuch einer physiologischen Pathologie des Herzens, Leipzig, 1866) gives the results of observations made on Marmots during their winter sleep as to the relation between the respiratory movements and the arterial pressure. In the Marmot, when in profound sleep, the contractions of the heart occur at long intervals, which, however, are much exceeded in duration by those which separate the respirations. By connecting the carotid artery with the kymographion (which can be done without waking the animal), a tracing was obtained from which it appeared that the mercurial column sank during the first third of inspiration, rose during the second two thirds, continued to rise during the beginning of expiration, and again fell during the remainder. Of these facts he gives the following theoretical explanation:—"The negative inspiration-pressure not only sucks air into the lungs, but blood towards the heart. The greater impletion of the heart enables it to propel more blood into the arteries, and increases its frequency, while its contraction as compared with its relaxation is prolonged. Expiration produces an opposite result; for it facilitates the emptying of the lungs of blood, and adds to the systemic pressure. But inasmuch as the heart becomes less and less full during expiration, the increase of pressure is limited to the commencement of the expiratory act, a smaller quantity of blood being injected into the arteries. At the same time the duration of the contraction diminishes, while that of relaxation increases" (p. 353). Here the author appears to attach much more importance to the direct influence of expiration than the facts warrant.

EXPLANATION OF THE PLATES.

In each figure the upper tracing is that produced by the lever connected with the Dynamometer, and expresses the variations of arterial pressure; the lower by the lever connected with the caoutchouc bag, and expresses the movements of air in and out of the chest.

In the arterial tracing three-tenths of an inch of vertical measurement correspond to one-tenth of arterial pressure. The breaks indicate synchronical points in the two tracings.

Plate XXIII. figs. 1, 2, 3, 4 & 5. Varieties of natural breathing: fig. 6 represents that form of breathing in which expiration commences with a prolonged whine.

Plate XXIV. figs. 1–4. Obstructed respiration: figs. 1, 2 & 3, partial closure of breathing-tube, the degree of obstruction being indicated by the shaded portions of the circles B, C, D; fig. 4, complete closure.

Plate XXIV. figs. 5 & 6, and Plate XXV. figs. 1, 2, & 4. Artificial respiration after subcutaneous injection of woorara: fig. 3, period during which artificial respiration was arrested; figs. 5 & 6, effects of single injections of air into the chest after several minutes' discontinuance of artificial respiration.

Fig. 1.

Fig. 2.

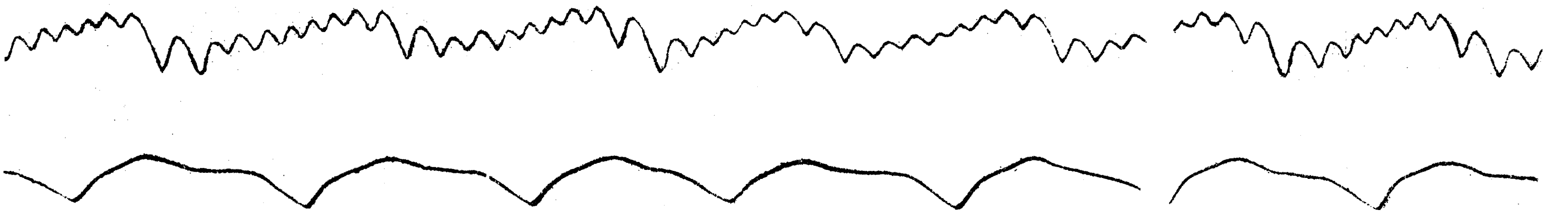


Fig. 3.

Fig. 4.

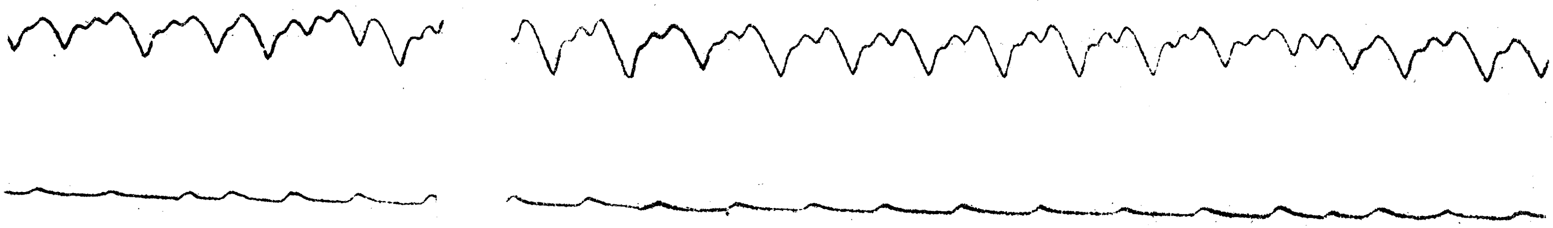


Fig. 5.

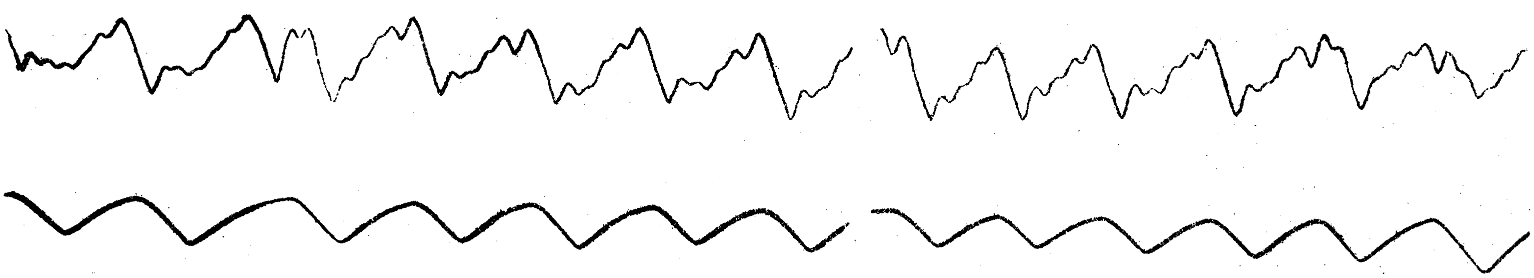
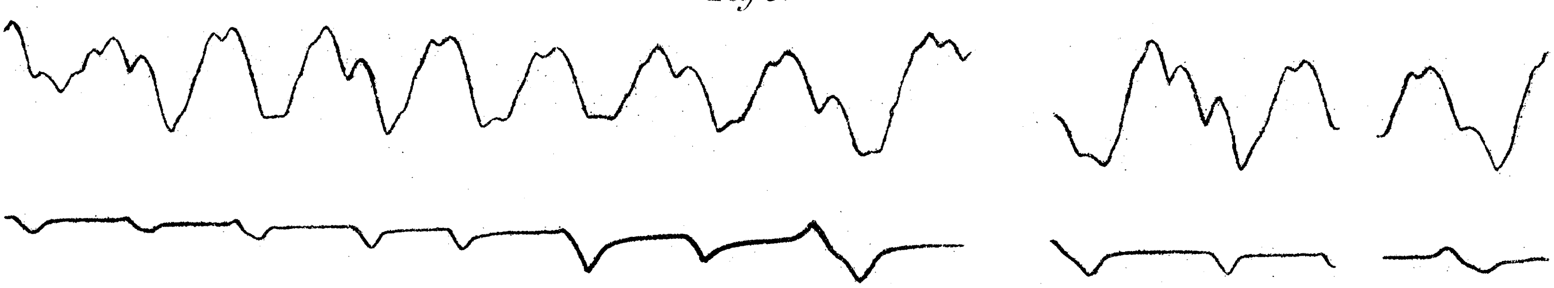


Fig. 6.



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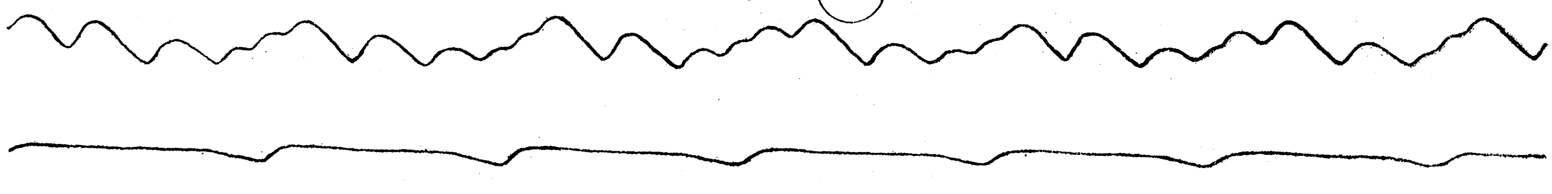
BY STEPHEN AYLING, 493, OXFORD ST. LONDON.

Fig. 1.



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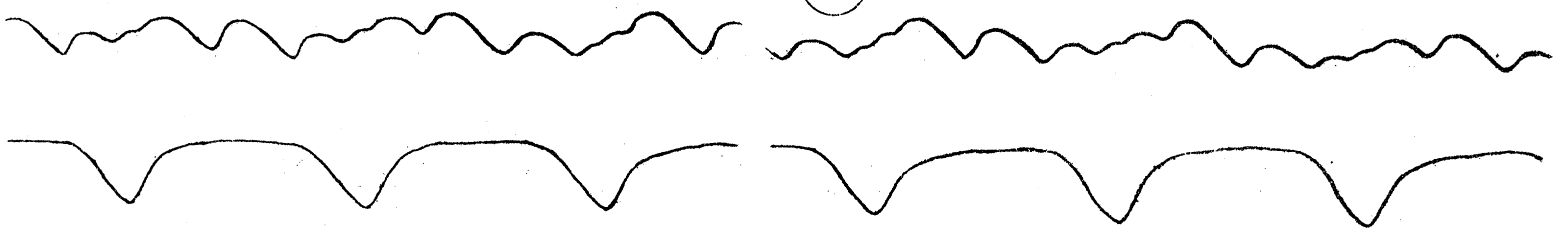

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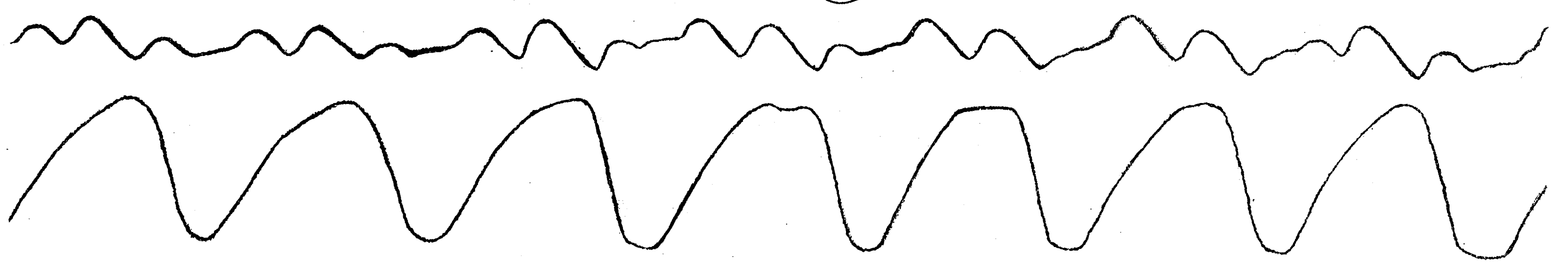

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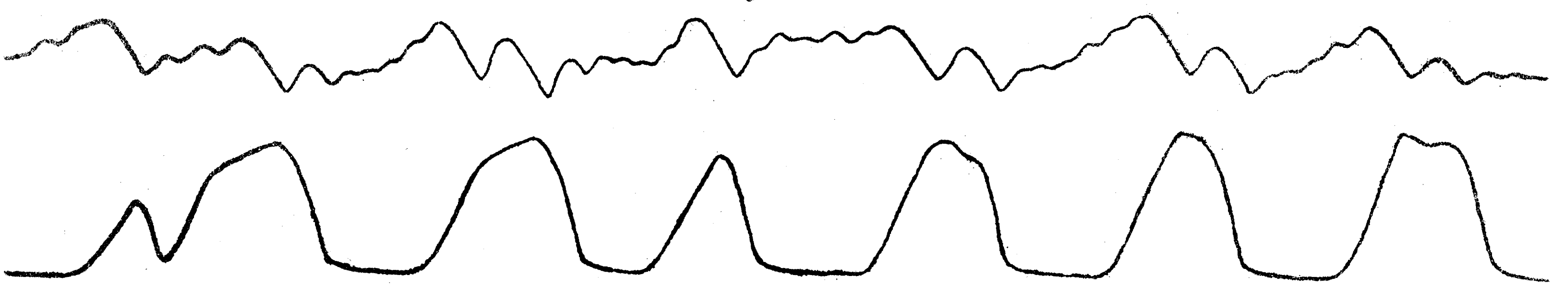

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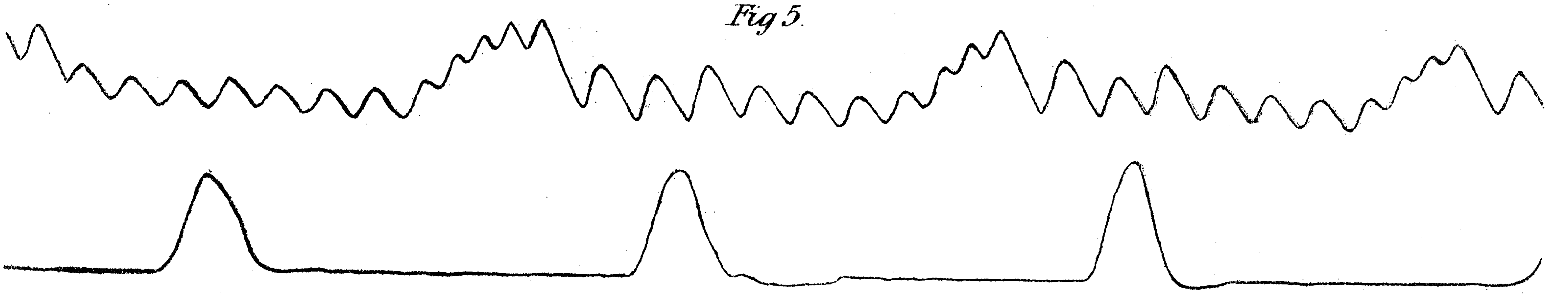

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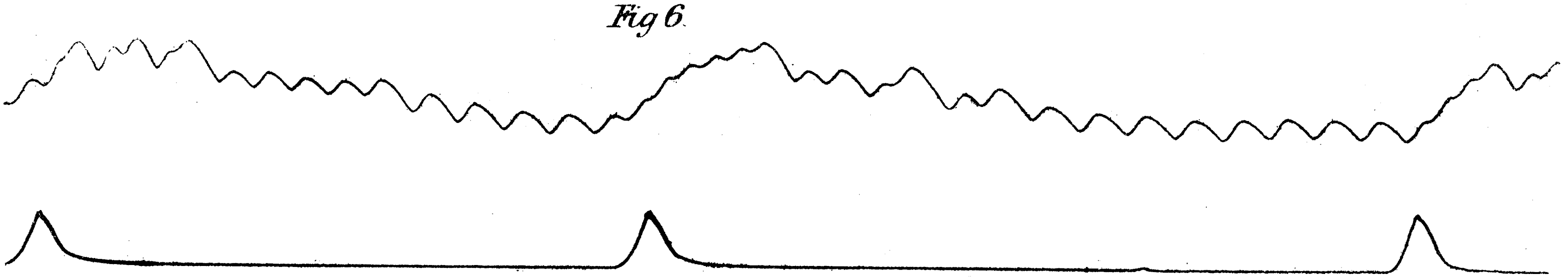

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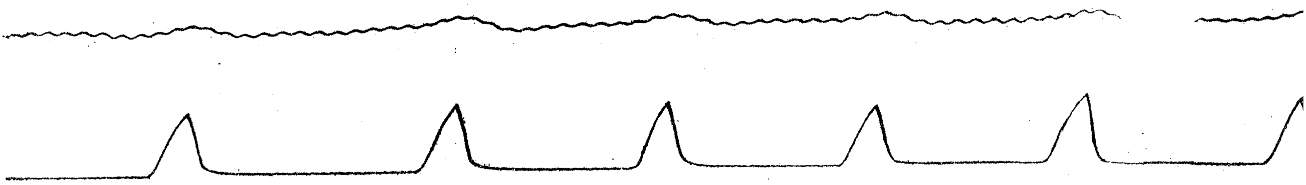
Fig. 1.



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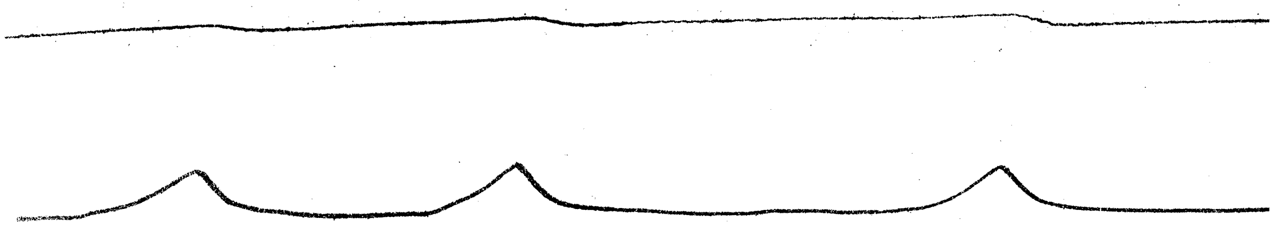

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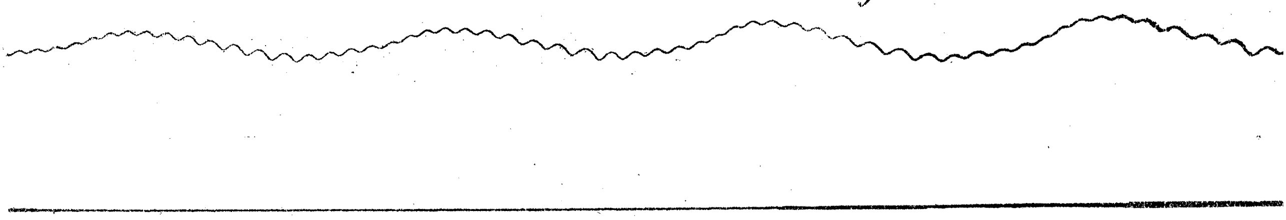

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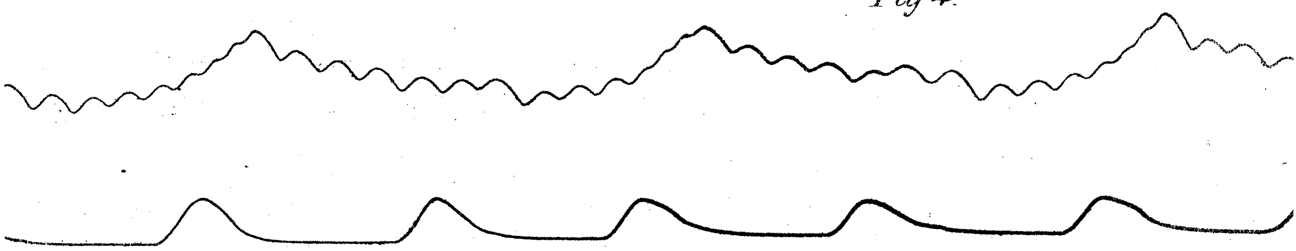


Fig. 5.

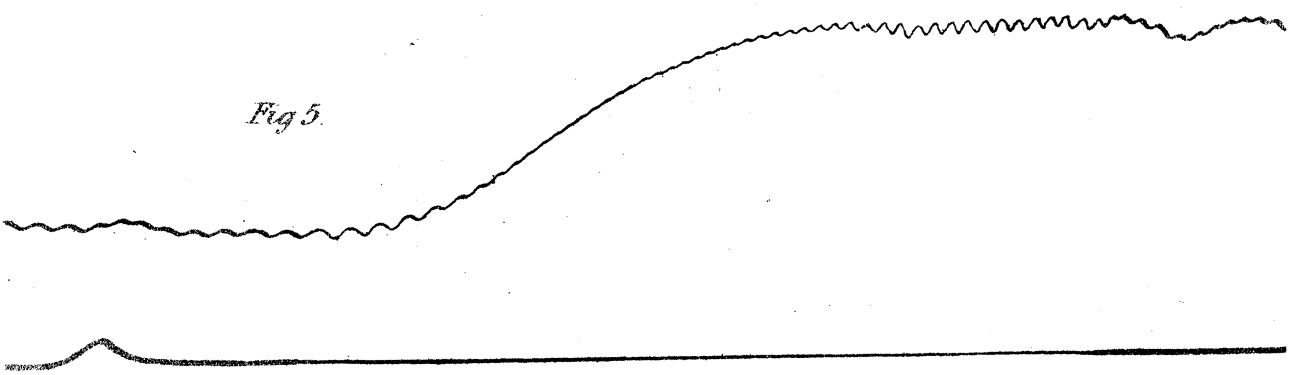
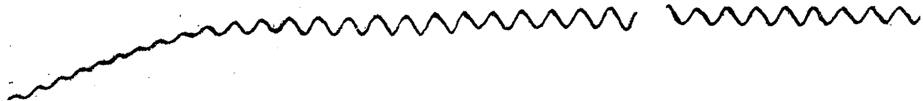


Fig. 6.



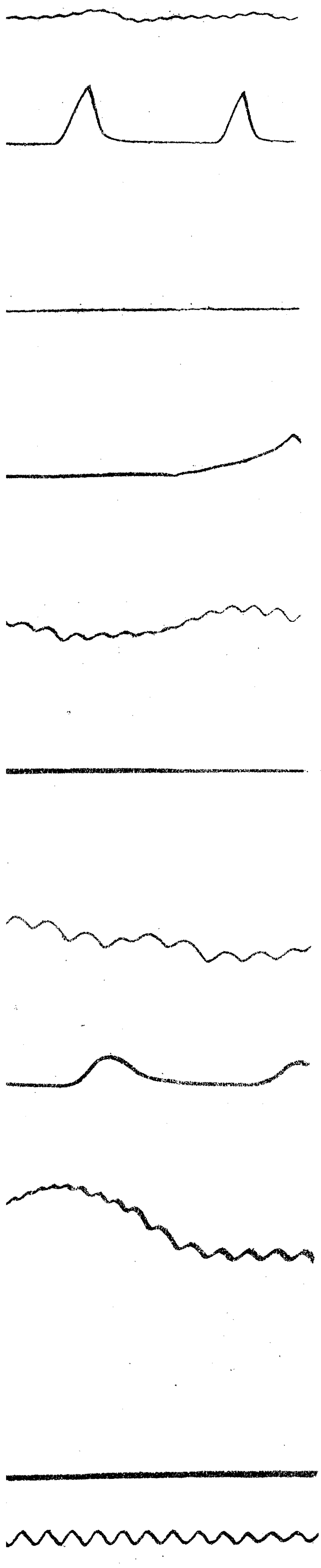
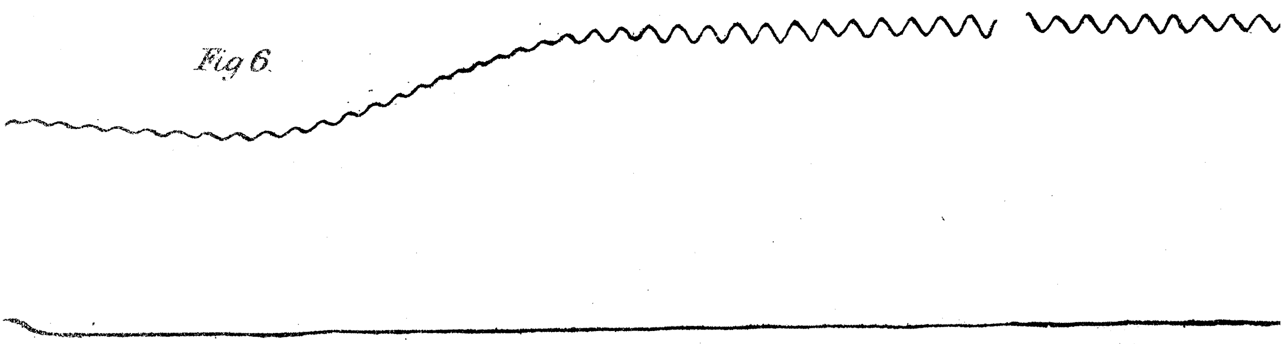


Fig 6.



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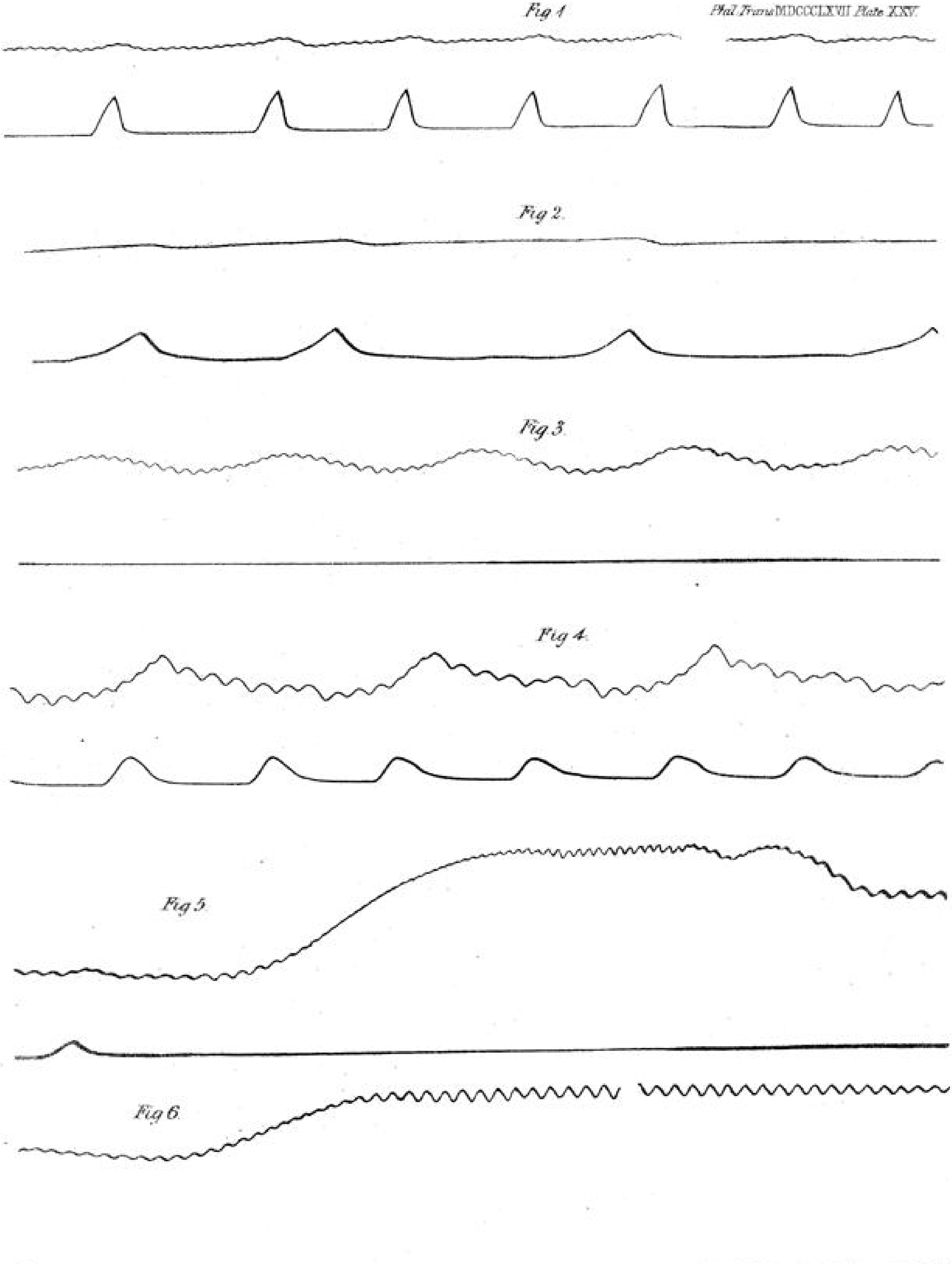
Fig 1.
Fig 2.
Fig 3.
Fig 4.
Fig 5.
Fig 6.