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ON THE

ACTION OF THE MUSCULAR COAT

OF THE

BRONCHIAL TUBES

IN

RESPIRATION.

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ON THE ACTION
OF THE
MUSCULAR COAT OF THE BRONCHIAL TUBES IN RESPIRATION,
AND ON THE
EXCITING CAUSE OF INSPIRATION AND OF EXPIRATION.

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The office which the muscular coat of the bronchial tubes fulfils in respiration is not at present decided. There is little doubt that it tends to prevent over-dilatation of the tubes by reacting against any undue pressure on the part of the air they contain, precisely as the muscular coat of an artery reacts against the blood-wave when forcibly propelled. We may admit also that it reacts partially and spasmodically for the removal of irritating matter from any part of the tubes, as in bronchial cough. But has it, as its discoverer, Reisseisen, considered, any regular and rhythmical action in the movements of the lungs during respiration? Does it relax with each inspiration, and contract with each expiration? Such an opinion is discountenanced by the latest writers on physiology.* To attempt to show that it is not without arguments in its favour is the object of the present communication.

It is observed by Müller, that if the muscular coat of the bronchial tubes acted rhythmically in respiration, it would have to be under the influence of the will, which is not the case; and, moreover, that the purposes supposed to be fulfilled by such rhythmical contraction would be answered equally well by elasticity. Dr. Carpenter remarks, that "it can scarcely be imagined that the bronchial tubes should, by any power of their own, contract and

* Müller, Dr. Carpenter, Dr. John Reid, Dr. Kirkes.

dilate uniformly with the contraction and expansion of the chest, unless their muscles were equally subject with those of the thorax to the influence of the nervous system, which all experiments concur in showing not to be the case."* It is urged, again, that the only contraction to be seen in experimenting on the bronchial tubes is a tonic, regular contraction, which lasts for some time. "The muscular fibres of the bronchial tubes," said Dr. John Reid, "are endowed with that kind of contractility termed *simple contractility*, which manifests itself by more slow and prolonged contractions and relaxations than that of the voluntary muscles and the heart."†

I have, then, to show,—firstly, that it is not necessary that the bronchial muscular coat should be directly under the control of the will for the purpose of taking a regular part in the act of expiration; secondly, that elasticity would not answer the purpose here fulfilled by muscular contractility; thirdly, that it is not proved that the fibres of the bronchial muscular coat are incapable of the alternating form of contraction, *i.e.*, of quick contraction and quick relaxation; fourthly, that the bronchial muscular coat is under the influence of the nerves to an adequate extent.

1. Müller observes, "The glottis is dilated during inspiration, and contracted during expiration. The bronchial tubes are also dilated during inspiration, and contracted during expiration;"‡ and yet immediately afterwards he states, "it is probable that the bronchial tubes and trachea do not contract and dilate rhythmically during the movements of respiration. Had they this power it would be quite an isolated fact; for although the hepatic duct presents rhythmic contractions, they are quite independent of the will, while, if the bronchi contracted and dilated synchronously with the other respiratory movements, their action, like that of the other parts engaged in respiration, must also be subject to the will, and it is highly improbable that the branches of the efferent tube of an internal viscus would be thus under the influence of the will."§ To this we may reply, that the diaphragm, and other respiratory muscles, present rhythmic contractions, which are not "quite independent of the will;" the heart, rhythmic contractions

* "Principles of Human Physiology," 2nd edition, p. 456.

† Art. Respiration, "Cylopædia of Anatomy and Physiology."

‡ "Physiology," by Baly, vol. i., p. 345. § Ibid, p. 347.

which are quite independent of the will, and therefore that the more or less subordination to the will cannot be the condition on which rhythmic action depends. Moreover, the trachea and bronchi are as much afferent as efferent ducts, and are employed with a constancy and a regularity which distinguish them from any other visceral tubes. It is probable that the muscles of the glottis are only indirectly under the control of the will, and *their* alternating action in respiratory and vocal efforts is admitted. To this extent the muscular fibres of the trachea also are certainly controlled by the will in the production of high vocal notes, and in voluntary coughing. Many involuntary muscles are indirectly influenced by the will through the medium of voluntary muscles. It is not necessary for the tracheal or bronchial muscles to be controlled by the will in any other way than this. By willing to fill the tubes with air until their fibres are on the stretch, or by drawing in particles which irritate the lining membrane, we can at pleasure excite their contraction. By suspending our breath after a moderate expiration we can probably for a short time at pleasure suspend their action.

2. Elasticity opposes any change from its condition when unexcited. It recoils equally from a maximum and from a minimum size. The lessening of the bronchial tubes below their medium size is as much opposed by the elasticity of their walls, as is their dilatation above it. Elasticity tends to maintain their medium calibre, but not either to increase or to lessen this. If, therefore, expiration be at all expedited by lessening of the bore of its tubes, as it undoubtedly must be, something more than mere elasticity is required. In viewing elasticity as equally opposing undue dilatation and undue diminution of the air passages, and as being inoperative so long as the tubes remain of their medium size, we refer to the elasticity of the *walls of the bronchial tubes only,* and to this acting towards or from the centre as regards the tube. Like arteries, the bronchial tubes during health are always kept on the stretch in their length, whatever the amount of expansion or contraction of the lung; and the elasticity of the general parenchyma is never allowed to reduce the lung to the size to which it contracts it on opening the thorax after death. After the fullest possible expiration the general elasticity would reduce the lung still more were it not opposed. Under all circumstances, therefore,

the general elasticity of the lungs, and the *longitudinal* elasticity of the tubes, oppose inspiration and favour expiration. But the bronchial tubes, though on the stretch in the longitudinal direction, are not so in their transverse diameter. The elasticity of their walls cannot lessen the calibre of the tubes any more than it can increase it. What there is of concentric elasticity in the walls of the bronchial tubes is opposed equally to a full expiration and to a full inspiration. In this mode of acting the bronchial tubes precisely resemble arteries. On exposing a small artery, it will contract to half its natural size, in virtue of its muscular coat. It could not do this by its elasticity solely.

The *longitudinal* elasticity of the bronchial tubes can assist expiration merely by drawing the air-cells towards the larger tubes, by the mutual compression of the air-cells which this entails, and by maintaining the internal surface of the tubes smooth and free; not by any such tightening of the circumference of each tube as will diminish its calibre. Yet, to render the expulsion of the breath complete and equable from every portion of lung at the same time, this latter action of uniform lessening of the bore of the tubes is what is chiefly required. Every one has noticed how much more readily an empty sponge is made to fill itself with water than a wet one to empty itself, in consequence of the difficulty of compressing at the same moment every individual portion of it. A like compression of every individual portion of the lung is required for perfect and full expiration. And here the compressing force is placed within the sponge, and lines all its tubes, in the form of a muscular coat.

The structure of the bronchial tubes teaches so much. It is true that the larger bronchi have plates of cartilage, the elasticity of which operates in the transverse direction of the tube; but these are so far from being always kept on the stretch, like the longitudinal elastic fibres, that their principal use is to maintain an open condition of the tubes under all circumstances, by resisting alike concentric and eccentric force. Nor would any considerable lessening of the larger tubes assist expiration. Unless, indeed, it occurred subsequently to progressive lessening of the smaller and more peripheral tubes, it would obstruct the egress of air from the air-cells. If muscular contractility be the agent for lessening the tubes, we find a correspondence with the requirement in the greater

development of the bronchial muscular coat in the smaller tubes; but if elasticity be the agent, this correspondence is wanting; elastic tissues exist in largest proportion in the larger tubes. In the larger tubes we find plates of cartilage, and longitudinal elastic fibres thickly and closely packed. Between these, and separating them, is placed a thin layer of unstriped muscular fibres, which, as they are not firmly attached to the plates of cartilage, can have but little influence over them; and next to the longitudinal fibres, the mucous membrane. In the smaller tubes the cartilages no longer exist; the longitudinal elastic fibres are all placed lengthwise, never across the tube; they branch at their extremities, and intertwine to an extent sufficient to ensure their keeping together, but not sufficient to enable them to either lessen or enlarge the tube in the wall of which they are situated. The circular muscular fibres form a thicker and stronger layer than in the large tubes, external to and surrounding the longitudinal elastic bands. Arrived at the commencement of a vestibular passage, or passage of entrance to several air-cells, the muscular coat ceases abruptly, whilst the longitudinal elastic fibres spread out from under it, and stretching in curved loops over each bunch of air-cells, form the frame-work upon which the thin basement membrane, with its delicate pavement epithelium, is spread to constitute the wall of an air-cell. It results from this arrangement that the openings of the air-cells can never become closed by any action of the muscular coat. Had the muscular fibres been the most internal, their energetic contraction might have closed up (like a sphincter) the door of the vestibule, and instead of dyspnœa, a fit of asthma would have caused asphyxia. As it is, the effect of the contraction of the circular muscular fibres is to press upon the longitudinal elastic bands; these, being always on the stretch, by opposing the pressure, render it uniform and equal throughout the tube; and by their expanding to embrace the air-cells at the point where the termination of the muscular coat leaves a ring of muscle with a free margin, convey the muscular compression on to the walls of the cells, and effectually prevent any ring-like constriction. Thus the channel of the tubes is kept smooth and free, and the openings into the air-cells patent, under every degree of expansion and contraction of the lung.*

* Did space permit, it would be easy to show the bearing which these considerations have on the mechanism of the production of emphysema.

We may conclude that elasticity alone is inoperative in reducing the bore of the air-passages to anything less than its medium condition; that no especial elastic tissue is so arranged as to answer such a purpose; that muscular fibre is so arranged as to answer precisely this purpose, and no other.

3. To ascertain the fact, whether the alternating form of contraction could be excited artificially in the muscular coat of the bronchial tubes or not, the following experiments were made.

Experiment 1.—The trachea and the right vagus nerve were laid bare in a full-grown rabbit. Both needles of an electro-magnetic machine, when applied to the front of the wind-pipe, occasioned general convulsive movements of the body, and spasmodic choking and gasping. Both needles applied to the trunk of the vagus caused similar effects to a still greater degree, shrieking and great pain. The heart beat violently. So far the electricity had evidently been conducted to other tissues by the moist and warm surfaces to which the needles were applied. These effects having subsided, the trachea was divided, and a flexible tube inserted into its lower portion. By directing the free end of this tube against the flame of a spirit lamp, the number, force, and length of the expirations could be readily observed. Galvanism to the vagus nerve quickened respiration, and rendered it tumultuous, disordering the action of the thoracic muscles. The number of expirations was counted for periods of ten seconds. Without galvanism, the expirations were now at the rate of 150 per minute. The right vagus was next isolated over a smooth slip of dry wood, and two slender needles stuck through the nerve into the wood, but not through it, so as to place the intervening portion of nerve in an electric circuit, without the electricity being directly conducted to other animal textures besides the nerve. The nerve was then divided above the wood, near to the base of the skull, so as to prevent any reflex excitement through the root of the vagus. No alteration in the respirations immediately followed this division of one vagus. The galvanic poles were now applied to the needles. The expirations instantly rose to 171, and became more forcible. Without galvanism, the expirations then fell to 72. The other vagus (the left) was next divided in the neck, both nerves being now separated from the brain. With galvanism applied as before, the expirations were at first short, quick, and 138; they then became slower and more

lengthened. In a few minutes they were, without galvanism, 42; with galvanism, 72. The most marked effect of the galvanism upon the expiration, now that this was slower, consisted in the more prolonged, continuous, and forcible expulsion of the air.

The thorax was now opened on the right side, so as to expose the right lung and the right side of the heart. The expirations without galvanism were, 48; with galvanism to the left vagus, 54. No movement whatever could be excited in the exposed right lung, which of course was collapsed, either by galvanism to the right vagus or to the lung itself. The heart ceased to manifest any increase of action from galvanising the nerves in the neck, but contracted with increased vigour and frequency on galvanising the ventricles. The opposite side of the thorax was now opened. Of course respiration instantly ceased, and could not be re-excited by galvanising one vagus, both vagi together, lungs by themselves, or lungs and vagi. No effect now followed the application of galvanism to the bronchial tubes, either whilst the lungs were warm and *in situ*, or after their removal from the chest.

Experiment 2.—The trachea and left vagus were laid bare in a large fowl. Expirations were now 48. On applying galvanism, as in the preceding experiment, to the trachea, vigorous convulsive movements of the whole body, and rapid quivering elevations and depressions of the wind-pipe ensued; so rapid that it could not be ascertained satisfactorily whether the individual rings of the trachea were approximated to each other or not. The trachea was then cut through, a tube inserted, and galvanism applied to the lower portion. This affected equally the upper and the lower segment of the wind-pipe, proving that the electricity was conducted by the warm, moist muscles on which both portions of wind-pipe rested. The left vagus was now isolated over a slip of wood. Expirations without galvanism, 48; with galvanism to the nerve, 72. With galvanism to the trachea only, expirations 54, and general struggling. With galvanism applied again to the left vagus, expirations 60; without galvanism, 48.

The vagus was not cut through in this experiment.

After death, galvanism was immediately applied to the heart, stomach, trachea, bronchi, and substance of lung, but produced no effect.

Experiment 3.—A large rat was held under water. It was 80 seconds in drowning. The rat was taken out of the water, and its trachea was divided. A tube was fastened into the lower portion of the trachea, and its orifice was held under water at some depth. On opening the front of the chest, the pressure of the water in the tube prevented the egress of the air from the lungs, which therefore did not collapse. Galvanism was then applied to both vagi at once, and caused immediate, sudden bubbling of air from the mouth of the tube under water. After this, no effect. The tube was then emptied of water, and the lungs were fully inflated through it, and the tube again submerged. According as the depth of the tube in the water permitted the resiliency of the lungs to operate or not, the air bubbled out spontaneously, but no further action could be elicited by galvanism applied to the vagi, to the trachea, or to the substance of the lungs.

Experiment 4.—Both lungs were exposed in a large frog. They rose and fell with each pulsation of the heart, but had no other movement. Mechanical irritation of their surface induced no contraction in the wall of their transparent honey-combed lung-sacs. When artificially over-inflated through the glottis, the lungs would return to their medium size, expelling the superabundant air, but this resulted from elastic recoil merely. Mechanical irritation of the vagi had no perceptible effect.

Examined with a half-inch power, whilst the animal was alive, the blood-globules were seen to stream through the vessels of the diaphanous walls of the lungs with great but very irregular rapidity. When the lung recoiled after its pulsational elevation, a momentary check occurred in the race of the blood-globules. In the larger vessels, this check caused the globules to oscillate; but in the capillaries it occasioned merely a more tardy rate of travel. If, however, the capillaries farther on had become impacted with globules, so as to become impervious, then the nearer capillaries leading to them also presented oscillation of the blood-globules. So long, therefore, as the whole net of capillaries is free, the course of the blood through them is regular and uniform in passing on, but not quite uniform as to rate of travel, being quickened by each contraction of the heart; whereas in the vessels larger than the capillaries the blood is not uniform and regular in passing on, but

gushes in a to-and-fro tidal stream, advancing more than it recedes with each systole of the heart. To equalize the stream and convert an intermittent into a steady and constant pressure, both the muscular and elastic properties of the coats of the arteries are doubtless called into action. This observation appears to answer in the negative a query, propounded by Dr. Charles Bell, viz., whether the actions of the capillaries in general do not receive a constantly repeated stimulus from the alternate flux and reflux of the blood-wave. It also demonstrates that the capillaries will be always equally full in a state of health, provided the circulation through them be unobstructed; but that their fulness will instantly become augmented provided any obstruction occur.

The check in the blood-wave in the smaller vessels (not capillaries) immediately preceded the pulsation of the heart, and accompanied the slight falling of the lung from its pulsational elevation. In point of time, it occupied about one part out of five. In the capillaries, the blood-globules were noticed to pass across the field in single file, each globule becoming elongated and somewhat dumb-bell shaped as it passed through a small capillary, and resuming its ovoid globular outline on entering a larger vessel. The walls of these small capillaries could not be seen at the focus employed.

The observation was continued for three hours. As the lung became dry from exposure, and the heart's contractions more languid, the lung appeared more and more congested to the naked eye. Under the microscope this congestion was found to consist in mere impaction of globules in the vessels, not in extravasation of globules or of *liquor sanguinis*, so far as could be made out. It does not follow that such would be the case in a similar state of congestion of the lungs in the living body, warm and moist.

Experiment 5.—On exposing the lungs in a frog, they burst out and expanded by successive deglutitions of air to their maximum size. No appearance of anything like muscular reaction of the lung followed each gulp of air. On the jaws being held separate, the frog made a twisting movement, and the lungs immediately collapsed. As soon as the lungs had again become filled with air, galvanism was applied to both lungs at once. It occasioned general struggling and instantaneous emptying of the lung-sacs. Allowed

to become filled with air again, galvanism was applied to one of the lungs only: no effect.

Experiment 6.—Three frogs. It was tried to induce collapse of the lungs by galvanism. This effect always ensued when both lungs were galvanised together, so that the current of electricity passed across the body of the frog, and excited convulsive movements, but never so long as the galvanism was restricted to the walls of one lung. Galvanising the vagi had no perceptible effect. As in the preceding experiment, the lungs rose and fell with each pulsation of the heart. In one particular a correspondence was noted between the state of the circulation and the amount of pulsational elevation. The circulation was freest, and the rise of lung greatest, when the distension of the lung with air was to a medium extent. If the lungs were distended to the utmost, pulsational elevation was scarcely noticeable. If almost empty, the same. Under the microscope, the difference in rate of travel and in freedom of passage of the blood-globules, in accordance with the amount of distension of the lung with air, was equally well marked. When the lung was greatly distended the circulation through the capillaries was almost at a stand. When the lung was almost empty many capillaries were obstructed by the pressure of adjoining portions of the collapsing walls, and the circulation in others was more tardy. But when the lung was moderately full of air, the circulation was most free, most equal, and most rapid. It could not be made out whether the rate of capillary circulation was influenced by the purity of the air contained in the lung, that is, whether circulation was faster immediately after the ingestion of fresh air than after the air has remained in the lung-sac for some time, or the reverse.

It will be observed, in passing, that we have here by analogy a demonstration to the eye, of what experience has long since taught, that moderate exercise of the lungs promotes freedom of circulation through their blood-vessels, whilst inactivity of the lungs, and over-distension of them with air, equally oppose freedom of circulation, and thereby favour the production of congestion, or the augmentation of any which may already exist.

Experiment 7.—Both lung-sacs were removed from a large frog.

The animal lived for two hours, making frequent inspiration-like movements of deglutition.

Experiment 8.—Galvanism was applied to the exposed surface of the heart in three frogs. At first the pulsations were increased in frequency, maintaining their proper rhythm. Presently, the ventricles contracted slowly, until they were squeezed tight and firm, without any attempt at dilatation interrupting the contraction. They remained in this state for from 8 to 15 minutes, the galvanism being taken away. They then gradually relaxed, admitted blood from the auricles, and proceeded to pulsate rhythmically again. Galvanism, again applied, induced the tonic contraction as before. In two of the frogs this was done twice, in the third three times, after which the heart remained contracted and motionless, and refused any further manifestation of activity.

In this artificially induced persistent spasm of the heart in the frog, have we not the type of the cause of death in angina pectoris, and perhaps also in certain cases of suddenly fatal epilepsy?

We learn from these experiments, that the expirations can be notably quickened and rendered more forcible in birds and mammalia by galvanising the vagi; that in the frog, galvanism applied to the lung alone has no effect, but that if conducted to the spinal cord, so as to excite general movements and opening of the glottis, it then indirectly affects the lungs by opening their entrance-passage, and allowing their elasticity to expel the air they contain; that experiment thus confirms anatomical examination in deciding that there is no muscular tissue in the lungs of Batrachian reptiles; and that a muscle whose normal duty it is to contract in the alternating manner, viz., the heart, may be made, by over-stimulation, to assume the persistent tonic form of contraction.

The capability of the bronchial muscular coat to undergo the alternating contraction, which it must if it alternately contract and relax with every expiration and inspiration, is not demonstrated to the eye, but it seems to be all but proved inferentially. The general muscles of respiration were excited by galvanism applied to the vagi, even when these were prevented by division from acting as excitors through the medulla oblongata, and when precaution was taken to prevent the electricity from being conducted away from the nerves. We must assume that the galvanised vagi acted

centrifugally, and produced an impression of some kind on the terminations of the cerebro-spinal nerves distributed in the lungs, and induced through them excito-motory action of the respiratory muscles at large. What proof, then, do the experiments 1 and 2 furnish that the bronchial muscular coat was stimulated at all, since the excitement of the general respiratory muscles is enough to account for the increased frequency of the respirations? It will not, however, explain why the effect should be manifested chiefly by *ex*piration, rather than by *in*spiration. Under ordinary circumstances, any interference with breathing is first and principally shown by the inspiratory act, whilst in these experiments it was noticeably the expiratory part of respiration that was made more forcible by galvanising the vagi. I infer that the bronchial muscular coat was stimulated to contract, and that it did so rhythmically after its normal fashion, and that it was in consequence of the increased rapidity of its contractions thus induced that the expirations were increased in force, suddenness, and frequency. If it be objected that the bronchial muscular coat has never been seen to present any other than tonic contraction when exposed to view, we may reply that the conditions are then so opposite to the natural ones under which breathing is performed, that we have no right to decide what the muscle *cannot* do during health from what it *will* do when exposed to sight in a cooled and collapsed lung. In experiments on the stomach, Longet proved that the state of fulness or emptiness of the organ modifies to the greatest extent the kind and degree of movement excited by stimulating the par vagum. So may the emptiness of the bronchial tubes, and the removal of the general elasticity which is always operating in the normal condition, prevent the bronchial muscular coat from acting in its normal manner. In the preceding experiments, left undisturbed and unexposed, and in every respect, excepting in the application of a stimulus to its nerves, placed under its natural conditions, we have reason to expect that the bronchial muscular coat, if excited at all, would show that excitement by an increase of its normal mode of acting. Dr. C. B. Williams and other observers have established the fact of the contractility of the bronchial tubes, and Volkmann has found that this contractility is excited by galvanising the vagus. If, then, contraction were excited in the above experiments, it could not have been the tonic form of contraction. Nothing but alternate

contraction and relaxation will account for the augmented force and frequency of the expirations. Nor is the opposite view strengthened by the occurrence of tonic contraction (*i.e.*, spasm) of the bronchial tubes in nervous asthma. Here, the exciting cause is so intense that it may affect the bronchial muscular coat precisely as we have seen that over-galvanising will affect the heart in the frog, *i.e.*, it may induce spasm in a muscle which, under gentler and more normal excitement, would perhaps (like the heart) present the alternating kind of contraction. At all events, we can no more suppose that so inconvenient and distressing a condition as that of asthma represents the ordinary and healthy mode of contraction of the bronchial muscular coat, than we can infer the ordinary mode of action of voluntary muscles from the tonic rigidity of tetanus, or that of the heart from the tonic spasm of angina pectoris. And, admitting that spasmodic asthma furnishes an illustration of tonic contraction of the bronchial tubes, have we not an equally strong pathological illustration of alternating contraction, or clonic spasm, in the repeated convulsive expirations of whooping cough, and in certain varieties of hysterical cough?

4. The last objection, viz., that the bronchial muscular coat is not sufficiently under the influence of the nerves of respiration, provided my interpretation of the experiments adduced be correct, is no longer tenable.

Having endeavoured to dispose of the objections advanced against the theory of Reisseissen, I proceed to consider what may be stated in its support.

A strong argument by analogy is deducible from the fish, in which the normal movements of the respiratory organs may be watched. Respiration in the fish consists in the deglutition of water, as in the batrachian it consists in the deglutition of air. There is, therefore, no distinct inspiration and expiration. Still the process is divided into a stage of ingress, with open mouth and closed gills, and one of egress, with closed mouth and open gills; and the two acts are performed in rhythmical order, like the inspiration and expiration of lung animals. The hyoid apparatus acts as a piston to the common cavity of the mouth, pharynx, and gills. By its retraction when the gill outlet is shut, water is sucked through the open mouth. The muscles which retract the hyoid arch relaxing, the mouth is closed, the arch advances, the opercular covers press down against

the expanded gills, the branchiostegal valvular folds which closed the gill outlet are tucked up, and the water is driven out. Between the two rows of fringe-like processes which each branchial arch usually presents, a plane of well-developed muscular fibres exists. Judging from its anatomical connexions, this interbranchial muscle will move the two rows of gill processes upon each other, approximate them when separated, and compress the gill processes altogether against the inner boundary of the branchial chamber. Supposing that such muscular action were to operate during the ingress of the water, it would prevent the free access of the fluid to the surface of the vascular branchial fringes, and defeat the object intended. But supposing the gill processes to be separated to receive the influx of water, the interbranchial muscles being relaxed, the contraction of these muscles during the subsequent stage of egress of the water will expel the fluid from between the branchial fringes, and thus materially assist in emptying the recesses of the gill-chamber, and also by squeezing the water through the vascular fringes, bring the blood of the fish into closest contact with the aërating medium. May we not fairly assume that the interbranchial muscle of the fish corresponds to the bronchial muscle of the mammal; that the act of expelling the water from the gills corresponds to the act of expiration; and that the interbranchial muscle operates as an expiratory agent? It may be that there is a further analogy. Any particles of food or of other foreign matter which, having escaped the sieve-like sensitive valves placed at the pharyngeal openings of the gills, may have insinuated themselves between the vascular membranes of the branchial processes, will here excite irritation and excito-motory contraction of the interbranchial muscles to an extent sufficient to produce the ejection of the irritating particles into the sphere of the large current of water passing through the gills. If so, the process of expulsion will be the analogue of the cough of mammalia.—The expansion and closure of the gills and gill-fringes may be readily observed in the common gold-fish in a globe of water.

Granting the analogy, let us trace its consequences. The interbranchial muscle must ordinarily act in unison with the other muscles of expiration. Were it to hold the gill processes in close approximation during the act of inspiration,—so to term the stage of ingress of water,—it would prevent the application of the water

which is to purify the blood in the membrane which it bathes; on the other hand, were it to fail to contract after the water between the separated gill processes had become depraved by fulfilling its office, it would prevent a sufficient change of water at the next inspiration, and would perhaps allow the closing gill-covers to press together portions of the bronchial processes irregularly and unequally. Again, we cannot suppose the interbranchial muscles to exist merely for an occasional purpose but rarely required, and not to fulfil a constant purpose, for which their arrangement admirably adapts them. I assume, therefore, that they act rhythmically with every closure of the gill-covers, *i.e.*, with every act of expiration. In what does this rhythmical action consist? Merely in their fibres contracting every time they are stretched, ceasing their contraction as soon as they have effected it. And if we deny this we fall into a conclusion far more improbable, viz., that by elasticity and the action of the hyoid and opercular muscles, the gill processes are alternately opened and shut, separated and approximated, and yet that an extensive layer of muscle placed between each row of branchial fringes, during all this constantly recurring movement of the parts to which it is attached, remains passive. So, in mammalia, it is admitted that during every inspiration the glottis, trachea, and bronchial tubes dilate and widen, and during expiration contract and lessen. Unless, then, the tracheal and bronchial muscles do rhythmically contract with each expiration, and relax with each inspiration, we are forced to conclude that they are alike unaffected by stretching and shortening of their fibres; a conclusion opposed to the ascertained attributes of both striped and smooth muscular fibres.

The rhythmical contraction of the bronchial tubes is conformable with what we know of the physiology of respiration in general. How is it excited, directed, and controlled? The rhythm of the bronchial tubes must coincide with that of the respiratory muscles at large. We cannot voluntarily alter the rhythm of respiration, without wilfully affecting the external conditions of respiration, either by modifying the action of the muscles, the quantity and quality of the air, or in some other way the relation of the blood to the lungs. And if these external conditions be altered, respiration is altered, whether we will or not. Hence the rhythm of respiration depends more on external conditions than on the nervous

centre itself. The nervous centre is the governor of the process, but not the cause of it, and in its government it is largely dependent on the conduction of impressions from the acting organs.

We must seek, then, for the exciting causes of the rhythmical action of the respiratory muscles, not in the medulla oblongata, which is merely the controlling power, but in the external conditions which excite in succession the acts of inspiration and expiration. Respiration, as a double excito-motory act, requires an excitor for inspiration, and an excitor for expiration, so arranged that they shall alternate in their application, and consequently in their effect. This constitutes the rhythm. "What," said Dr. John Reid, "are the excitations which lead to the performance of the muscular movements of expiration? Do the same excitations that occasion the muscular movements of inspiration operate in the production of the expiration which immediately follows, so that they are to be considered two stages of the one and same muscular action? These are questions which we are not prepared to answer."* In most works on physiology, the exciting cause of expiration has not been made a subject of consideration, whilst many and various conditions have been assigned as the ordinary exciting cause of inspiration. Of these may be enumerated, the presence of carbonized blood in the vessels of the lungs; of carbonic acid in the air-cells; and of carbonized blood in the capillaries of the system at large, either superadded to one or both of the former conditions, or constituting in itself the exciting cause of the act of inspiration under ordinary circumstances.

Stating them as mere postulates, there are some grounds for considering that the ordinary exciting cause of inspiration is distension of the capillaries of the lungs with carbonized blood; and the exciting cause of expiration, the presence in the air-cells and bronchial tubes of unduly carbonized air.

That distension of the pulmonic capillaries with carbonized blood, and not the presence of carbonic acid in the air-cells, is the ordinary exciting cause of the act of inspiration, is presumable from the following considerations. In the fish, the sensation which excites the taking into the mouth of fresh water cannot depend on the presence of carbonized water in the gill-processes, since the gills have just been emptied of the used water. The presence in

* Loc. citat.

the branchial capillaries of venous blood requiring oxygenation is the only adequate condition we can find. In mammalia, the desire for inspiration immediately succeeds to the expulsion of the impure breath, at the moment when the lungs must contain the smallest proportion of carbonized air. The most urgent distress for fresh air attends disease in man, in which pulmonic engorgement prevents the access of air at all to a great portion of the lungs, or in which a sticky secretion clogs the air-cells and their vestibules. Here the desire for breath is greatest, whilst the amount of foul air in the air-cells, because of the absence of *all* air, is least; but the capillaries are gorged with venous blood, which cannot part with its pulmonic excretion. The presence of unduly carbonized blood in the capillaries of any part of the system, at all events, its presence in the medulla oblongata appears capable of exciting an inspiratory act, independently of the state of the lungs, as in the frog from which the lungs had been removed. If the like condition of the pulmonic capillaries be the ordinary excitor, we have a similarity in the conditions which act as excitors of inspiration in different parts of the system. But what proof have we, that under ordinary circumstances the state of the lungs has anything more to do in exciting the desire for breath, than that of any other part of the body? It would be strange if the instinct which points to the chest as the seat of the earliest feeling of desire for breath were altogether wrong in its indication. By division of one vagus the number of respirations is dropped about one-fourth. By division of both vagi at once the respirations are dropped one-half. I see no other mode of accounting for this than by considering that one great normal source of excitation of inspiration (viz., the lungs,) has had some of the wires of its electric telegraph to its nervous centre cut off, and that it can therefore send only an imperfect message to demand supplies. In this we see an illustration of the law that every reflex act is considerable in proportion to the sum of the excitement set up in the nervous centre, and this usually is in direct proportion to the number of nerve-fibres by which the excitation is conveyed. Cut through half of the excitor nerve-fibres, and other circumstances the same, the excitation is reduced by one-half, and the resulting movements become only half as forcible, or half as frequent. Now, did the lungs only share with the rest of the body in exciting the

sensation of want of breath, division of all their nerves (and the vagi do not constitute half of their nerves), would not produce the full effect which ensues from division of the eighth nerves. Conversely, through what other nerves can we quicken respiration in the same manner that it was quickened by galvanising the vagi in the experiments I have narrated? The vagi are the chief, though not the only excitor nerves proper to the lungs; as their irritation accelerates the frequency of the respirations, and their division greatly retards it, it seems to be proved that the lungs are greatly concerned in setting up the sense of desire for breath.

The following considerations support the opinion that the presence of carbonized air in the smaller air-passages and air-cells is the exciting cause of expiration. In the fish, the water is expelled from the gills as soon as it has received the excretion of the branchial membrane, *i.e.*, expiration occurs as soon as the water has become carbonized. In batrachian reptiles the air is expelled from the pulmonic bags after it has remained for an uncertain period undergoing admixture with the pulmonic excretion. In mammals, the desire to expire arises as soon as the fresh air inspired has had time to become depraved. The desire for expiration is intense in direct proportion to the length of time that breathing has been suspended, and consequently in direct proportion to the degree in which the air contained in the lungs has become impure, excepting only when the lungs happened to be contracted below their medium size when the suspension of breathing was commenced. Carbonic acid when inhaled induces closure of the glottis. It is a fair deduction that it would cause contraction of the tracheal and bronchial muscles if applied in strength to the membrane which covers them. If the carbonic acid of the breath so affect the bronchial muscular coat, as the contraction of that coat can only participate in the expiratory part of respiration, it follows that the presence of carbonic acid in the air-passages tends to excite one link in the chain of expiratory actions.

Is the effort of the bronchial muscular coat to contract one source of that sense of constriction in the chest which is felt on holding the breath too long after a full inspiration? If so, the sensation of muscular tension in the air-passages may assist in rendering the desire to expire air from the distended lungs more urgent. But this muscular tension is certainly not the first nor

the chief excitor of the act of expiration. Reptiles expire air without having any muscular texture in the walls of their lungs. Partly from this cause, but chiefly from their being cold-blooded animals, reptiles can hold their breath for a long and uncertain time. Having to remain under water for irregular periods, they would be only incommoded by possessing muscular lungs, which would tend to contract on the contained air as soon as this had become charged with carbonic acid. Mammals, on the other hand, require purer blood, and cannot expel carbonized air from their lungs too rapidly, or replace it too completely. Hence they possess muscular lungs.* When a rat drowns, bubbles of expired breath make their appearance in 30 or 40 seconds, whether the animal struggles or not. When a frog is submerged, bubbles of expired air may not rise for a quarter or half-an-hour, or they may rise immediately, just as the animal struggles or remains quiet. I infer that in the rat, the bronchial muscular coat contracts, and compels some air to escape; but in the frog, the lung-sacs having no muscular fibre to become excited, expel the air only when an accidental opening of the glottis permits its escape.

The non-existence of muscle in the lungs of the batrachian, where respiration is not regularly rhythmical, and its existence in those of mammalia, where respiration is regularly rhythmical, points out that the contraction of the bronchial muscle is at least not opposed to rhythmical action.

It has been ascertained that a stream of carbonic acid checks circulation in the capillaries. If the presence of carbonic acid in the air-passages thus checks circulation in the capillaries of the lungs, it of course tends to produce the condition of vascular fulness, assumed to be the exciting cause of inspiration. In this case the carbonized air will not only excite contraction of the bronchial tubes and other concomitant acts of expiration, but will also favour the occurrence of the next act of inspiration, by inducing the commencement of that fulness of the capillaries which, increasing, excites inspiration. Occasionally, indeed, it would seem as if

* Cetaceans can remain below water for a much longer period than other mammals, and yet possess muscular bronchi, but their normal frequency of respiration (in the whale) is not quicker than 5 or 6 per minute, and there is special provision made in the suprofical position of the larger bronchial tubes, as well as in the extensive retiform blood-sinuses, for preventing distress.

the two excitations were in operation together, and that, either, one prevailed because it became the stronger of the two, or else because volition interfered. Thus, after a moderate expiration, if a man holds his breath as long as possible, the immediate desire will be for inspiring. Here there are carbonized air to excite expiration, and capillary distension to excite inspiration. As the lung is but imperfectly filled, the latter condition predominates in intensity. The bronchial tubes having left off with expiration, are kept below their medium size; their contractility is tired out, and their elasticity tends to enlarge them up to their medium calibre. On every account the tendency is towards inspiration. But let the breath be held after a full inspiration, and the conditions are reversed. The expanded bronchial tubes tend to return by their elasticity down to the medium calibre, their stretched and specifically excited muscular coat tends to contract, the tubes and cells filled with air, which has become impure, occasion intense desire for expiration, and expiration ensues. If the breath be held at a medium amount of expansion of the chest, so that the conditions are evenly balanced, the subsequent act is that of inspiration or of expiration indiscriminately. By an effort of will we may interfere with these tendencies, because the voluntary movements of respiration are stronger than the automatic. By a strong effort, for example, after holding a full, but not the fullest inspiration as long as is comfortable, we may draw in a little more air with momentary relief, but our feelings prove that we are thwarting nature. The automatic arrangements are tending towards expiration, and expiration must follow almost instantly.

Thus, inspiration necessarily leads to the condition which is the exciting cause of expiration; and expiration necessarily leads to that which induces inspiration.

All tubular muscles appear to respond directly, without the necessary intervention of any nervous centre to the mechanical stimulus of distension; and all are paralysed by over-distension. It is doubtful with respect to the bronchial muscular coat, whether any amount of inspiratory force can call forth this characteristic. The inward rush of air finds so ready a diffusion amongst that which fills the air-cells that these more yielding structures are the parts to suffer from excessive force of inspirations, and intervesicular emphysema, not burst, or dilated, or palsied bronchial tubes is the

result. But if the contractility of the tubes be never excited by force of inspiration, the expansion by heat of air shut in by closure of the glottis may increase the tension of the tubes as well as of the air-cells, and this mechanical distension may excite the contractility of the muscular tubes, in addition to the other exciting cause of expiration, viz., the presence of carbonized air. I find, with the spirometer, that a very slow and protracted expiration after a full inspiration does not raise the cylinder so high as a more speedy expiration. In other words, there is more breath left behind in the lungs. Are the bronchial tubes tired of keeping up their contraction until all the reserve air is expelled? Of course, the vascular fulness becoming greater in proportion to the time occupied by the experiment, may render the desire to inspire irresistible before all the reserve air has been expired.

Under whatever circumstances, if mechanical distension of the bronchial tubes do influence their contractility at all, it will always operate on the side of expiration. Still any such influence is quite subordinate to that exercised by the presence in the air-cells of carbonized air.

After a full inspiration, I can hold my breath for a period represented by 4. Here there is the least carbonic acid relatively to the amount of air in the lungs, but the greatest mechanical distension of the air-tubes. After a moderate inspiration, for $1\frac{3}{4}$; after a complete expiration, for only 1. Here is the largest relative amount of carbonic acid, but the least muscular distension —there is rather muscular contraction—of the bronchial tubes. Provided a very full inspiration immediately preceded the last trial, so as to freshen up the residual air in the lungs, the time during which suspension of breath could be maintained was increased one-half. Here the degree of dilatation or of contraction of the bronchial muscular coat was the same as in the third trial, but the purity of breath was greater, and the period of its suspension was consequently greater also.

We must conclude, that although the state of dilatation of the air-passages which immediately precedes the commencement of expiration may, by stimulating the stretched muscular fibres to contract, co-operate as a secondary and subordinate cause of the expiratory act, yet the carbonization of the air in the lungs is the essential and primary exciting cause of expiration, and with the

degree to which the breath has become carbonized the desire to expire air directly corresponds.

The residual air left in the air-cells after a complete expiration is probably always more or less carbonized. It is fit for use when *minus* carbon; unfit when *plus* carbon; but some amount of carbon it must always contain. Consequently, it must either be the condition of *plus* carbon only which excites expiration, or otherwise the exciting cause does not make its impression in the air-cells, but solely in the tubes to which common pure air does reach with every inspiration. The exciting impression is probably made in both places, but the question cannot yet be determined.

Inspiration has many other exciting causes besides the state of fulness of the pulmonic capillaries with venous blood, which is here assigned as its ordinary cause; such are impressions suddenly made on any part of the skin or of the mucous surfaces, acute sensations, and mental emotion. But if the view here espoused be correct, expiration has no other primary exciting cause besides the presence of air in the lungs charged with the pulmonic excretion. × A frog, with its lungs removed, makes *in*spiratory efforts of breathing only. When the will does not interfere, the spontaneous effort of breathing made by a person struck, or surprised, is one of inspiration. As inspiration is a necessary preliminary to expiration, —as expiration is necessarily excited by air when inspired and used in the lungs, to render the act of inspiration liable to several different modes of excitation, is indirectly to confer the same privilege on expiration, although the proximate exciting cause of the two acts differs.

It is an advantage resulting from this ready and instinctive excitability of inspiration, that the body is instantly fitted for powerful muscular action by the very stimulus which renders that action necessary. For all active efforts a tolerably full and fixed chest is required as a fulcrum from which the muscles may act. Were the effort instantly excited by sudden sense of danger to be one of expiration, the body would be rendered mechanically as powerless by the emptying of the chest as it often is mentally by fear.

To recapitulate,—There seems reason to admit,

1. That, by their general elasticity, the lungs are always kept on the stretch, and tend to contract to a smaller size than is ever permitted during life. This, under all circumstances, is favourable to expiration.

× i.e. ordinary quiet expiration.

2. That by the elasticity, which acts transversely in the walls of the air-passages, the tubes are accommodated to the amount of air admitted into, or contained in them; but that, for enlarging the tubes for inspiration, and for lessening the tubes below their medium size for complete expiration, this elasticity is useless.

3. That the muscular contractility of the bronchial tubes, whilst, like the transverse elasticity, it resists over-dilatation during full inspiration, *can* reduce the tubes to less than the medium size, as is required in forced expiration.

4. That, inasmuch as forced expirations always alternate with inspirations, the contraction of the bronchial muscular coat must here be of the alternating kind, and not of the tonic persistent kind noticed in certain experiments.

5. That, if the bronchial muscular coat can thus contract rhythmically in forced expiration, there is no reason for denying that it so acts, to a less extent, in ordinary breathing. Considering, indeed, the constant interruption to quiet breathing in the daily occupations of every man, from exercise of the voluntary muscles generally, and of the voice, from variations of temperature, and from mental causes, it is little probable that any part of the machinery required for forced respiration is quite unemployed during ordinary breathing.

6. That, as far as our knowledge will permit, the objections to such a view have been shown to be without sufficient foundation.

7. That the exciting cause of inspiration in ordinary breathing is fulness of the capillaries of the lungs with carbonised blood, but that there are many other auxiliary and occasional exciting causes of inspiration.

8. That the sole and exclusive exciting cause of expiration is the presence of unduly carbonized air in the lungs.

In conclusion, these views, if correct, are not devoid of practical interest. For an application of a portion of them, I must refer to the ingenious remarks of Dr. C. B. Williams, under the head of "Asthma, Paralytic Dyspnœa, and Dilatation of the Bronchi."*

* "Library of Medicine," vol. iii., from which I must quote the following, as more explicitly disclosing Dr. Williams's own view than any other passage I have met with. "It is probable that the contraction of the circular fibres of the bronchi, excited by a certain degree of foulness of the air that is within them, is an essential part of natural expiration."—p. 90.

The mere existence of the muscular elastic and cartilaginous textures which enter into the structure of the bronchial tubes, will dispose us to admit the influence of Gout and Rheumatism on bronchial affections. And the admission, that the bronchial muscular coat co-operates in every expiration, supplies us with an additional reason, were any wanting, for endeavouring to render bronchitic attacks as short as their naturally tedious course will permit, and for taking every care to prevent relapses in a very relapsing disorder. Seeing that the effect of inflammation is, first to paralyze, then to soften and destroy muscular fibre, and to spoil elastic tissue, the effect of bronchitis in producing defective expiratory power, local dilatations of the bronchial tubes, or vesicular emphysema, is susceptible of explanation on merely mechanical principles. So also may fatty degeneration of any part of the bronchial muscular coat give rise to local dilatation, by furnishing a weak and yielding spot in an elsewhere contracting tube.*

* As Mr. Rainey has proved with respect to fatty degeneration of the walls of the air-cells in (one form of) vesicular emphysema.