CHEST MOVEMENTS AND THE INTERCOSTAL MUSCLES*

By W. B. Primrose

To the anaesthetist, no bodily movement is so important as that exhibited by the breathing, as it provides information concerning the condition in which the unconscious patient may be at any particular time and also signs by which the administration of the anaesthetic has to be regulated. This being so, it is strange that of the many efforts to analyse chest movement, none seems to have given complete satisfaction, and the matter is to-day still in the position described by McKendrick in 1888 as "very confused". Robert Gesell (1936), in a more recent work on the respiratory muscles, indicates this confusion with reference to the intercostal muscles alone, and the subjoined list given by him after Luciani (1911) is worthy of note.

(a) Both external and internal intercostal muscles are inspiratory. (Borelli, Senac, Boerhaave, Winslow, Haller, Cuvier, Duchenne.)

(b) Both kinds of muscle are expiratory. (Vesalius, Diember Brock, Sabatier, Beau and Maissac, Longet.)

(c) The external intercostals are inspiratory, the internal are expiratory with the exception of the intercartilaginous portions. (Spigel, Vesling, Bayle, Hamburger, Hutchison, A. Fick, Martin and Hartwell.)

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The intercostals are of no great importance in regard to the movements of the ribs: they serve rather to regulate the tension in the intercostal spaces, and to reinforce them during inspiration, impeding their retraction by the increased negative intra-thoracic pressure. (Henle, Meissner, Brucke, von Ebner, Landois.)

To account for such diversity of view, it is necessary to examine the interpretation of chest movement as given by the anatomist, since this has always been accepted as sound, certainly as reasonable, and has always been taken as the starting point of the many physiological researches into the problem of chest movements.

From comparative studies of body-wall structure, the anatomist has been led to believe that the bilaminar intercostal muscles, being so similar in appearance and relationship to the bilaminar series of such simple forms as the earthworm, operate in a similar manner, that is, that the two muscular layers alternate and oppose each other in action and so account for the two phases of breathing. The fact was never noted, however, that while the physical conditions presented by the worm demanded the opposing actions of a circular and a longitudinal body-wall musculature, those same conditions were not present in higher coelomate forms in which a different body-wall physiology obtained. In these, although a laminated system of muscles was also required, it had to carry out quite different functions. The failure to note this difference of function arose from the devotion of morphologists to the idea of metameric segmentation of the body. This is a scheme or plan based entirely upon appearances presented by serially repeated parts in the so-called segmented coelomate animals, and from want of demonstration of the actual existence of the condition, the idea has now fallen considerably into disfavour, especially as its use in expre
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ing fundamental body structure has led to confusion in this problem of chest movements and others also. With this in view, the approach to the understanding of chest movements must be made from direct observation uninfluenced by any artificial preconceptions which have never been able to demonstrate actual function.

When radical mastectomy was commonly performed for cancer of the breast, the exposed chest provided excellent opportunities for close observation of the external intercostal muscles as these were always undisturbed. Two movements were apparent, namely, the to-and-fro movement of the chest as a whole, and frequently, the insucking of the intercostal muscles with each inspiration. These intercostal muscles appeared to offer little resistance to the negative intrapleural pressure set up by the descending diaphragm, and they certainly did not appear to contract rhythmically as was shown if some of the fibres were accidentally cut: the incision so made merely gaped without rhythmical alteration, indicating a state of tonic contraction of no great power or apparent purpose.

A further observation made in the course of some cerebellar operations was the contraction of the cut ends of the reflected occipital muscles during inspiration. In this operation the patient was lying prone and unconscious. The muscles, epimeric according to anatomical grouping, seemed to be strange associates in the respiratory act which is carried out by hypomeric muscles normally. This served to show that breathing, rendered difficult by the prone position, could call into play any muscles that could exert any influence upon the chest, however indirectly, and quite independently of any morphological arrangement. It also presented clear visible evidence of muscular contraction about which there could be no doubt. When, from
evidence of fatigue in these long operations, the patient was suitably supported, giving the diaphragm unrestricted freedom in its descent, the occipital muscles no longer acted in this way.

It has also often been noticed that when artificial respiration has been called for in the course of anaesthetic practice, that the physical effort required in this procedure was out of all proportion to the effects produced, particularly in elderly subjects. This seemed to show that the chest tended to fixation and did not contribute greatly to breathing, and this in spite of a freely movable system of diarthrodial joints between it and the vertebral column.

These observations stimulated interest in the motive power exercised upon the chest, especially as the intercostals did not appear to provide any; and, as other experimenters have found, the problem is centred upon these muscles which all have desired to see actually working.

With this end in view, a beginning was made by the direct observation of the breathing muscles of a dog—greyhound—and of those other body-wall muscles considered to be related to breathing. Recalling the visible contraction of the cut ends of the occipital muscles in the above-mentioned cerebellar cases, similar contraction was looked for by cutting the fibres of the various muscles. No action of any kind could be found, even when the fibres were examined under some magnification (20 diams.). The intercostals, which in the greyhound are well developed, gave no indication of any contractile effort although the chest exhibited its normal to-and-fro movements. It was also not possible to discern any movement of the ribs, each to each, for in spite of skeletal limitations they are permitted a small degree of independent movement which their intrinsic muscles would show if they acted with any
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vigour. With the exception of the diaphragm, which was obviously in action, the same was observed with regard to all the other muscles examined in this way. Even the sterno-mastoids, which could be the most powerful elevators of the chest, were quite inactive, and the abdominal muscles did nothing to retract the chest. The negative findings of this simple examination seemed to show that none of the body-wall muscles credited with respiratory function from their anatomical associations with the chest appeared to act with any physiological purpose.

An investigation with a similar purpose was carried out by Sharpey Schafer and MacDonald in 1925, but it was combined with the use of the string galvanometer to detect muscle potentials. While the latter part of the experiment was not successful, the observations given in the account are of interest.

These workers isolated a group of three ribs with their intercostal muscles from the sternum and from the adjacent ribs by section of the intercostal muscles before and behind and from sternum to vertebral column. They recorded that the isolated group kept pace with the rest of the chest and they were at a loss to account for this, since they expected that the external intercostals would show evidence of contraction in advancing the ribs with inspiration and that the internal muscles would show the reverse movement. Nothing like this seems to have happened, for the paper ends with these words: "We had supposed it would be easily possible to resolve this question of the active participation of the internal intercostals in the expiratory movement of the ribs by the employment of the string galvanometer, but have met with unexpected difficulties in applying that method, and have not yet succeeded in
entirely overcoming these difficulties." To these experimenters, the difficulties of assessing costal movement have arisen from two sources. In the first instance, they did not succeed in obtaining visible contraction of the muscles; and secondly, they were dominated by the anatomical convention which required that these muscles oppose each other in action to account for inspiration and expiration as separate muscular acts.

This experiment, in spite of its unsuccessful issue, appeared to be worthy of repetition, but with some modification. It seemed that if the ribs exhibited gross movement as a chest, then that movement could be stopped by section of muscles other than the intercostals, since these had obviously failed to influence the movement of the ribs in the above experiment. It was decided to follow this line of investigation.

For this experiment rabbits were used: they were intubated through tracheotomies for control of respiration and also anaesthesia. The ribs of one side, the left, were exposed with their intercostals and detached from the sternum, with the exception of the first, in order to avoid damage to the subclavian vessels. This was done by cutting through the costal cartilages close to the side of the sternum so that these ribs would have no contact with that bone. Isolation of the group of ribs was completed by section of the first intercostal muscles from front to back.

Arranged in this way, the experimental ribs with their intercostal muscles moved to-and-fro, keeping pace with the sound side, although having no contact with it. The pectoral and the serratus muscles were reflected and the abdominal muscles were detached from the lower costal margin, as was also the diaphragm. These sections, however, made no difference, the ribs continuing to move
Chest Movements and the Intercostal Muscles in perfect order as a chest. Finally, the intercostals were cut from front to back as far as the angles of the ribs. The normal uniform movement of the ribs continued, and their forward thrust could be distinctly felt as before. This seemed to point clearly to the fact that the intercostals had little to do with the visible movements of normal breathing. Some other muscular agency was providing the power.

Another rabbit was prepared in the same way so as to display the intercostal muscles; but this time the dorsal spinal muscles having attachments to the ribs were removed. It was desired to expose the levatores costarum as being the muscles most closely identified with the ribs and the vertebral column. On finding and dividing these, the ribs and their intact intercostal muscles at once came to rest. This seemed rather surprising, knowing that our own levatores costarum are small and feeble muscles quite incapable of producing this degree of costal movement. In fact, Keith (1903) regards them as acting upon the vertebral column. Enquiry at the Department of Anatomy, Glasgow Veterinary College, revealed the fact that in all the veterinary mammals the levatores costarum are relatively large and fleshy in the adult.

This statement is in keeping with that of Markwald (1888), who, writing on movements of respiration in the rabbit, stated that the diaphragm is not essential to life in adult rabbits, as these show a considerable degree of thoracic breathing. Rabbits under four to six months of age, however, die as they have not gained the full use of costo-vertebral muscles.

A peculiar and most fortunate accident occurred during this experiment. The tracheal cannula proved to be a trifle too large and the trachea split slightly. This necessitated the use of a smaller cannula, which was inserted, but it proved to be inadequate for normal breathing and so set
up dyspnœa. The effect of this upon the muscles that were being examined was remarkable. The intercostals, which had always been at rest, now contracted with great vigour, pulling the ribs strongly together with each inspiration and allowing them to relax with each expiration. Along with this activity, the infra-hyoids and pectoralis minor muscles were seen to be in active and simultaneous contraction. This may also have included the scalene, which is single in the rabbit, but this was not actually observed. MacKenzie (1919) believes that this muscle acts upon the neck. Of the other muscles, sterno-mastoid, pectoralis major, serratus anterior and the abdominal group, no sign of activity presented itself even under these conditions of urgency.

Reviewing these experiments briefly, the first rabbit showed clearly that the ribs, free to move, were not being acted upon by their intercostal muscles, otherwise they would have been crowded together by the external intercostals on inspiration. There was also no tendency for them to be actively separated by any muscles, least of all by the internal intercostals, which are supposed to draw them backwards in expiration. Neither of these muscles were in action even although the lung on that side was collapsed. The rabbit was in no way dyspnœic and there was therefore no urgency as regards breathing. The second rabbit showed where the power for inspirational movement of the ribs came from, the diaphragm not being there to assist. It also showed that the two intercostals acted together, and all as a group under strong stimulation which recalled the similar action of the occipital muscles. In view of the visible action exhibited by all the inspirational muscles, it would appear that they take very little part in this function and that only when compelled to do so.
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From the point of view of anatomy, these results, so far as the intercostals are concerned, are to be expected. The intercostals are unlike any other body-wall muscles in that they are bounded on all sides by thoracic and vertebral skeleton, so that when they act, they exhibit a closed system of forces. In virtue of this, they can only act upon points within that system, which is to say, upon the ribs themselves. These, not being particularly free to move owing to their sternal attachments, are merely pulled upon, giving a stiffening effect to the chest which provides a firm base for the attachments of the greater limb-girdle muscles and the diaphragm. In doing this, the intercostal muscles would actually reduce the capacity of the chest by a trifle: it might be better to say that they prevent undue expansion of the ribs and intercostal spaces in face of the expanding lung. The old idea that the crossed disposition of the fibres of these muscles indicated opposing functions is insupportable as the resultants of their contractions would always be in the lines of the mutual approximation of the ribs.

The electronic investigation of the muscles of respiration by means of a two-beam oscillograph followed very conveniently upon these experiments, and the table overleaf gives the results. These are generally in agreement with those of Robert Gesell (1936) who has worked extensively on this subject.

This method of investigation, probing as it does into the activities of almost individual muscular fibres, has its limitations. It indicates the surge of tonicity without displaying actual contraction, and as tonicity by itself does not perform gross function, the method by itself does not explain very much concerning chest movements. Much the same applies to the findings of Bronk and Ferguson (1935)
<table>
<thead>
<tr>
<th>Muscle</th>
<th>Description</th>
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<tbody>
<tr>
<td>Latissimus dorsi</td>
<td>Silent under free and obstructed breathing.</td>
</tr>
<tr>
<td>Pectoralis major</td>
<td>Silent except for postural tone on being stretched.</td>
</tr>
<tr>
<td>Pectoralis minor</td>
<td>Inspiratory, especially if dead space is increased or breathing obstructed.</td>
</tr>
<tr>
<td>Serratus anterior</td>
<td>Inspiratory in quiet breathing; strong expiratory in obstructed breathing.</td>
</tr>
<tr>
<td>External intercostals</td>
<td>Inspiratory.</td>
</tr>
<tr>
<td>Internal intercostals</td>
<td>Inspiratory, but anterior portion may show expiratory rhythm.</td>
</tr>
<tr>
<td>Sterno-mastoid</td>
<td>Silent under both conditions.</td>
</tr>
<tr>
<td>Infra-hyoids</td>
<td>Inspiratory.</td>
</tr>
<tr>
<td>Scalene</td>
<td>Inspiratory.</td>
</tr>
<tr>
<td>Rectus abdominis</td>
<td>Silent unless stretched, giving postural tone.</td>
</tr>
<tr>
<td>External oblique</td>
<td>Silent unless stretched, giving postural tone.</td>
</tr>
<tr>
<td>Internal oblique</td>
<td>Expiratory rhythm.</td>
</tr>
<tr>
<td>Transversus abdominis</td>
<td>Expiratory rhythm somewhat weaker.</td>
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</table>

who studied by the same means the impulses in nerve fibrils passing to muscles (intercostals). While their results are indisputable, they bear little relation to gross muscular movement which is the purpose of all these experiments and upon which knowledge is required.

These workers in this field have made no mention or allowance for two important features in their experiments. The first is the variable effect of general anesthesia upon muscular activity. Of this, the anaesthetist is fully aware from experience of fixed doses of drugs upon muscles capable of acting involuntarily or reflexly. This accounts very largely for the variable effects mentioned by Gesell (1936) for the intercostals of eight dogs. Gesell's findings in these dogs have led him to interpret them as individual differences in the breathing pattern. This view does not appear to be tenable, as it seems clear that such a uniform and massive act, as inspiration undoubtedly is, cannot be accomplished by such feeble muscles as the intercostals acting so variably and erratically as he has shown them to do. His
results point much more to the idea that the intercostals are not greatly concerned in the uniform acts of breathing, which have all the indications of concerted action. The second feature that may seriously modify these experiments is the age of the animal, a fact impressed upon the writer in the course of this investigation.

It so happened that for the earlier experiments, rabbits of six months or a little over were used; also a cat used was young although not a kitten. The dogs used were all greyhounds about four years old. The reason for the latter uniformity is that about this age, these animals begin to fail in first-class racing against younger ones and often exhibit bad temper against their rivals. In licenced tracks, these animals are usually destroyed. We were therefore dealing with young dogs which, with the other young adult animals used, showed chest movements at their best.

In a confirmatory experiment at a later date, a fully grown rabbit was asked for and this was produced—an elderly doe. Upon exposure of the chest, this was seen to be quite immobile and was useless for our purpose. Keith (1903) also mentions that the chest of the dog does not move to-and-fro: he evidently has been looking at a dog of unknown age, but certainly not young.

In this we are only seeing in other mammals what we know so well for ourselves concerning athletic prowess. After the mid-twenties it declines, possibly with the declining mobility of the chest which has been developed to the fullest extent to maintain the great demands of a rapidly developing muscular system. When this is attained, the movements of the more specialized individual small muscles such as the levatores costarum and intercostals decline, and with age, this may go on until practically only the diaphragm is left to provide active inspiration, as was found in the elderly rabbit.

The experiments described have therefore yielded visible evidence of the nature of intercostal action and of the activities of certain other muscles concerned with inspiration. No such activity was discernable with regard to expiration although the oscillograph indicated this function for muscles of the abdominal group. Obstruction to the breathing did not have the same effect on the expiratory muscles as upon those of inspiration. This can be verified clinically. A nose-breathing patient under general anaesthesia will exhibit strong inspiratory efforts which include
that of the sterno-mastoid on closing the nares, but there is no corresponding expiratory effort although such powerful muscles exist for this purpose.

The departure from the prevailing view of intercostal action indicated by these experiments is probably best accounted for by a reference to the development of so-called segmented structure in annulosemata forms.

In a paper (Primrose, 1920) dealing with the evolution of the vertebrate endoskeleton, it is pointed out that water is the first substance to be used as an endoskeleton in early animal organization; and in order to make use of this fluid material, especially in vermiform types, a new tissue makes its appearance as a step in evolution. This is the mesoderm of embryology. In the simple coelomate animals of vermiform shape such as the archannelid, Polygordius, two strips of this tissue grow in between the gut tube and the skin, which latter has an annulated appearance suggestive of that of respirator tubing and for precisely the same purpose (fig. 1). Very soon, a series of cavities begins to appear in each strip from before backwards. The inner or visceral layer applies itself to the gut-tube while the peripheral layer goes on expanding until it comes to lie under the skin, the cavities enlarging along with it. The skeleton of water, or hydrostatic skeleton as it may be called, occupies these cavities and, when fully developed, it appears as a bilateral series of water vertebrae which occupies almost the entire body. The body wall muscles which overlie them differentiate into an outer circular layer which is broken at the septal limits of every segment of skeleton and an inner longitudinal layer which extends the length of the animal as several narrow bands. By their actions upon the incompressible but fluid skeleton, they produce locomotion. The visceral layer of this
Diagram showing two stages in the development of Polygordius neapolitanus (after Woltereck) from the spherical trophophore larva. The annulated body grows down from the lower pole of the larva and mesoderm grows as two strips into this between the gut tube and the skin. The mesoderm acquires cavities as seen in the later stage which develop as the locomotor organ.
mesoderm applies itself to the gut-tube and differentiates the two layers of muscle characteristic of all higher forms for the propulsion of its contents.

When this arrangement of skeleton and muscle is supplied by serially repeated vessels and nerves from common trunks, we recognize, not a condition of segmentation of the body, but the development of an entirely new organ consisting of many serially repeated parts. This arrangement, on account of its extent in occupying nearly all the body, has given rise to the original misconception that the body was itself segmented. This new organ may be called the "locomotor organ" to indicate the principal function it performs for the animal.

This segmentation, which is restricted to the water skeleton, is the solution of a serious problem in coelomate organization, for water, free in a general coelomic cavity, would be unmanageable by any kind of muscles and would also constitute a grave danger to the vermiform animal owing to the risk of strangulation of its body during flexion. The arrangement of the body-wall muscles is that required physiologically to operate a fluid but incompressible skeleton of water vertebrae.

The prevertebrate chordates are characterised by the possession of a different kind of endoskeleton. This is the notochord. As an axial skeleton giving support and stability, especially to the dorsal neural tube, it is highly efficient, but its relative lack of flexibility, possibly due to its bulk and turgidity, appears to be a hindrance to the function of locomotion, which requires free flexibility of the trunk as a whole. The forms possessing this skeleton in an unmodified form either do not habitually leave the bottom of their muddy habitat like Amphioxus, or they have to depend upon a parasitic life like the lampreys: yet
they all possess a well-developed locomotor organ which only provides a small degree of free locomotion.

To overcome this difficulty of rigidity, the somites of mesoderm, in which form we now recognize the representative of the primitive locomotor organ, invade the notochord in such a manner as to produce a jointed axial skeleton which retains the original properties but adds the essential feature of flexibility. With this change, and with suitable musculature for a chondro-osseous skeleton, efficient locomotion became accomplished in the various vertebrate groups.

In principle, vertebrate form comes to consist of an elongated cylindrical shape maintained by an axial skeleton and its processes, integrated and overlaid with a muscular body-wall which encloses the viscera, many of which are highly resilient. This tubular body-wall which may show lamination of its muscle into from one to three layers can now only perform one function, namely, compression of the contents of the cavity it encloses, and use must be made of this single function by all the body-wall activities met with in vertebrates. Of these, breathing comes to be an essential function and, with the exception of the mammalia, is based upon compression of the body-wall. This act provides active expiration which is the feature of all these animals with the several variations suitable for the needs of each group. The bird in flight shows this principle of respiration most clearly as the lungs are kept passively filled during rapid forward motion and are emptied by abdominal compression.

Compression has been the feature of body-wall musculature since it first appeared in the worms, but it must be noted that these required compression in two directions acting upon an incompressible water skeleton. The muscle
was therefore arranged to do this. In the higher forms with a general coelomic cavity, general compression only is required, and to effect this, the body-wall musculature largely gives up its segmental or intercostal arrangement, its laminae arranging their fibres in a decussate manner so as to spread the grouped action of the muscles evenly over the entire cavity. A serial or peristaltic action could have no effect upon a general peritoneal cavity. The Annelida merely present a special instance of body-wall compression which serves to emphasize the fallacy of the idea of metameric segmentation of the body.

The physiological principle of body-wall compression as the fundamental act of breathing has proved efficient for all the vertebrates up to the mammals; but these, with a changed and greatly increased physiology, make demands for oxygen upon the principle of active expiration which cannot be met by existing musculature. A new principle of muscular action and of respiration has to be found to maintain these new conditions.

This change of respiratory principle has been effected by the introduction of a new structure developed in the septum transversum which, until now, has been occupied entirely by the developing heart and its great veins. This septum, originally extra-embryonic in position, is taken into the body of the embryo and it is in this that secondary mesoderm makes its appearance for the purpose of producing a muscular diaphragm which grows beneath the developing heart and lungs. The special function of this new muscular sheet is to provide an improved oxygen supply by means of active inspiration, a complete reversal of the physiological principle that has been adequate for all the lower vertebrates. The need for this new muscle is strong evidence that the pre-existing body-wall muscula-
ture, intercostals, etc., is quite unable to provide efficient respiratory function as is so generally believed.

Having reached this point in this brief survey of the chief points in the history of segmented muscle, it will be apparent that this kind of muscle has never played any part in the function of breathing. Segmented muscle is entirely locomotor and may be seen to act in this capacity in the snakes (Owen, 1866). When breathing began to make demands upon the body-wall musculature, this had to give up its segmented character and become laminated as sheets to provide active expiration. While the mammal has retained this it has, in addition, developed a new muscle and a new principle of breathing: it has adapted it also to a chest that still retains the primitive segmented characters, the intrinsic muscles of which, although bilaminar, still only move one rib relatively to another, and that only when most necessary to help other muscles in their inspiratory efforts.

This reference to locomotion brings to light another point, and that is the explanation as to why there are so many large limb-girdle muscles attached to the chest-wall, each anatomically capable of acting upon it, but which, under normal conditions, act from it as a fixed base. The chest, particularly in man, as has been stated, is not meant to move extensively in spite of the arrangement of the thoracic muscles and the elaborate system of diarthrodial joints between it and the vertebral column. These latter are, of course, all parts of the locomotor system, and it will be recalled that flexibility of the axial skeleton is an indispensable requisite for efficient locomotion and that this was the original reason for the segmentation of that skeleton. With few exceptions, this principle is general among vertebrates, the joints being there to allow of
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undulating flexibility of the spine during locomotion while the chest remains relatively fixed.

This fixation of the chest is often met with, and to an embarrassing degree, when recourse has to be made to artificial respiration. It is so often apparent that little is achieved by a considerable expenditure of work upon a chest that is not meant to move, especially in the elderly. How very simple is the proceeding when the skeleton is left alone and inflation carried out, either by the conventional anaesthetic apparatus, or, wanting such aid, by mouth-to-mouth inflation (through a gauze filter). Only action upon the flaccid diaphragm will produce satisfactory results in all cases.

From this account of the intercostal muscles, it may be seen that the notion of the paralysis of the intercostals as a sign of deepening anaesthesia (Guedel, 1937) does not exist in fact, as these muscles, even when tense, do not act visibly with clear breathing. The insucking movement seen is phrenic in origin as has already been explained and its diminution is a sign either of weaker action of this muscle as anaesthesia deepens or is due to dilatation of the larger bronchi facilitating respiration. Further, the intercostals are much too deeply situated and are entirely covered by much heavier muscles to show possible activity of their own.

The other important movement of the chest upon which comment may be made is that of circumferential expansion. This occurs passively as a direct result of the angulation of the ribs to the vertebral column. In the case of the second to the fifth inclusive, Keith (1903) points out that the articulations favour the so-called "bucket-handle" movement. It also results from phrenic action. The expansile movement is due to the expansion of the
lung as the descending diaphragm forces it to occupy the enlarging thorax. While the diaphragm is descending, much of the abdominal resistance it encounters facilitates elevation of the chest which the expanding lung exploits fully, even against the tension of the intercostal muscles which limit the "bucket-handle" movement. This is clearly seen in the trans-thoracic operation for gastrectomy. During the exposure, the left side of the chest shows only to-and-fro movement along with the other side. On closure, however, when the lung is finally inflated and the skin wound closed, the expansile movement reappears. During the operation, there is no sign of compensatory movement as breathing is free with adequate oxygenation. Generally, there is no expansile movement of the chest if the lung, for any reason, cannot be filled.

Keith, in his paper on the mechanics of breathing, gives a detailed osteological and arthrological account of the thoracic ribs, and shows that from the sixth to the tenth inclusive they are much more fixed than those above. This difference of anatomy is reflected in the living subject under general anaesthesia when, for any reason, respiration becomes obstructed. The natural heave of the chest and abdomen becomes replaced by an in-drawing of the upper chest and an out-pushing of the abdomen as a result of vigorous phrenic action. The lower thoracic region is observed to be almost at rest by comparison. This see-saw movement is characteristic of completely obstructed breathing.

Of the abdominal muscles, these have been found to contribute a little to normal quiet expiration. This, however, only represents a trifle of their available power for this purpose and almost requires the oscillograph to indicate their activity in this function. The lack of visible effort
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has led to the belief that expiration is mostly passive and due to the slight recoil of tonic muscles. Their action in quiet breathing may be seen in cystotomies for removal of the prostate or large calculi in thin elderly subjects. Some of these exhibit a markedly scaphoid abdomen with a chest fixed in inspiration giving a strong concave curve to the recti muscles. When the incision is made for access to the bladder, the separated recti may be seen to be slightly pulled apart by the laminar muscles attached to their sheaths, and this occurs with each expiration. This muscular activity, so often increased by coughing, would appear to be the cause of the difficulty met with in getting cystotomy wounds to close satisfactorily.

Another movement of the abdominal musculature has been observed on a few occasions. This was a wave of contraction seen to pass down the recti abdominis muscles with each expiration. The cases were urgent and for immediate appendicectomy. The first was a well developed young male under light anaesthesia with chloroform which produced very quiet breathing; the second was a similar young female who showed the movement to a lesser degree. This movement is difficult to interpret as it is so rarely seen, but the likelihood is that the local abdominal pain, somewhat severe, reflexly altered the nervous control in this way to avoid the more painful effects of general abdominal compression.

While this treatise has been principally concerned with observations made upon the unconscious subject, it must not be forgotten that breathing is powerfully influenced by the will in the conscious, and that almost any combination of body-wall muscles, particularly the most superficial postural ones, can be brought to bear upon the chest to effect respiration under abnormal conditions. The subject of acute asthma can no longer perform locomotion or do work, but by fixing his limbs he can exert much of his locomotor and prehensile power upon his chest; and in this
effort there are few muscles that cannot be used to some extent, both inspiratory and expiratory. These accessory muscles are brought into action to supplement the diaphragm when its power becomes overtaxed. Their use is abandoned when it is no longer required.

In view of the foregoing, mammalian breathing comes to be in principle a very simple act, although so many interdependent parts are involved in all the variations of its working. An entirely new muscle has been evolved for operating a new principle of respiration and is formed during development for the sole purpose of providing an oxygen supply by active inspiration. Normally, in mammals, there is no equally strong act of expiration in spite of the anatomical arrangement of muscles credited with that function. The great abdominal muscles always associated with expiration provide a little of this, but are much more designed, in the case of man, for doing work under conscious impulse as in the lifting of weights when they, as body compressors, operate strongly with a chest fixed in inspiration by a closed glottis. MacKenzie (1919) points this out. In this connection, it should be noted that the external oblique muscle in the pronograda is a strong flexor of the lumbar part of the trunk for fast locomotion and has no attachment to the ilium; whereas in man, the ilium cuts into the side of this muscle, giving it an extensive attachment as an additional compressor of the abdomen. This power of doing work by compression of the body is a compensation for the loss of much locomotor function in man associated with his erect posture. His body-wall, however, still exhibits the features fundamental to locomotion, but, at the same time, he is permitted to use his locomotor or limb muscles for a variety of other purposes. In common with other mammals, his respiration
Chest Movements and the Intercostal Muscles represents the latest stage in the evolution of breathing and, in this, the intercostal muscles have come to play a very insignificant part. This conclusion brings the idea developed here concerning these muscles into line with those expressed by Henle, Meissner, von Ebner, and Landois (1911), who assert that “the intercostals are of no great importance in regard to the movement of the ribs; they serve rather to regulate the tension in the intercostal spaces; to impede their retraction by increased negative intrathoracic pressure; and to reinforce them during inspiration.” This view is further supported on clinical grounds.

In cases of hemiplegia and other unilateral cerebral lesions normal respiratory movements are not interfered with, but forced respiration does show inequality on the two sides (Walshe, 1951). This would indicate that normal breathing movements are quite involuntary and independent of cerebral control, and that voluntary efforts to intensify breathing are directed from the highest level. It is of interest to note that the recession of costal structure from the anterior parts of the lower six intercostal muscles has allowed these portions to become highly specialized as compressors of the abdomen and, in consequence, they have come under voluntary control and are capable of a high degree of physical training, which cannot be said of the intercostal muscles. More than ever, then, do the intercostal muscles, limited as they are by costal and other skeleton, remain in a primitive physiological state playing a very minor part in the respiratory act, which normally is carried out by the more deeply placed extra-thoracic muscles in association with the diaphragm.

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REFERENCES


Walshe, F. M. R. (1951), *Personal communication.