CHAPTER 7

ACT OF BREATHING: THE VENTILATORY PUMP*

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In order to breathe, we must continuously contract and relax our respiratory muscles about 30,000 times a day, or a billion times for a lifetime of 90 years. Such extreme demands are not made of any other skeletal muscles. The respiratory muscles move the parts of the chest wall that form the boundaries of the thoracic cavity, either enlarging or contracting its volume and thereby ventilating the lungs. This ventilatory pump is obviously essential for life. The main function of the lung is to exchange gas, whereas the main function of the ventilatory pump is to replenish the alveoli with fresh air and to expel alveolar gas from the lung.

VENTILATORY PUMP

The ventilatory pump consists of the following: (1) the respiratory muscles, which expand and contract the thoracic cavity; (2) the compartments of the chest wall that the muscles displace when they contract, namely the rib cage and abdomen; (3) the cortical and brainstem centers that control the respiratory muscles; and (4) the intervening neural connections.

What are the respiratory muscles, and how do they accomplish their task?

Ignoring the upper airway muscles, which contract to maintain airway patency, the main respiratory muscles are as follows: (1) the diaphragm, divided into its costal and crural parts, which have different actions, anatomic origins, and cervical segmental innervations; (2) the abdominal muscles, of which the transversus muscle appears to be the most important in breathing; (3) the inspiratory muscles of the rib cage, including the external intercostal muscles, the parasternal muscles, the scalene muscles, and the sternocleidomastoid muscles; and (4) the expiratory muscles of the rib cage, including the internal intercostal muscles and the triangularis sterni muscle. A complete description of the respiratory muscles can be found elsewhere in this book (see Chapter 22, “Actions of the Respiratory Muscles”).

The compartments displaced by the respiratory muscles are the rib cage and the abdomen. Outward displacements of the abdominal wall and expansion of the rib cage are inspiratory, and vice versa. When these two compartments move in opposite directions, with expansion of one and contraction of the other, there is very little interaction between the two. However, what interaction there is cannot be ignored, as is discussed below.

A substantial part of the internal surface of the rib cage is directly apposed to the diaphragm. As a result, one can model the rib cage as being composed of two subcompartments, the part that is apposed to the lung, the pulmonary rib cage, and the part apposed to the diaphragm, the abdominal rib cage. The boundary between the two compartments is at the level of the xiphisternum at functional residual capacity (FRC). Ribs 1 to 6 are tightly attached to the sternum and thus form part of the pulmonary rib cage. Ribs 7 to 12 are loosely attached to the sternum through considerably longer costal cartilages. The parts of them below the level of the xiphisternum form part of the abdominal rib cage.

AGENCIES ACTING ON CHEST WALL COMPARTMENTS

The reason why it is useful to describe the rib cage as two compartments is that the forces acting on each are quite different. The pulmonary rib cage is exposed on its inner surface to pleural pressure (Pp) over the surface of the lung. As Pp becomes more negative with inspiration, it acts to contract the pulmonary rib cage. To prevent paradoxical displacements, inspiratory rib cage muscles must be recruited. These act on the pulmonary rib cage, but not on the abdominal rib cage. Of all the inspiratory rib cage muscles, only the external intercostal muscles are attached to both the pulmonary and abdominal rib cage compartments, and the fibers inserting on the ribs in the abdominal compartment only become activated at high levels of exercise. Under most circumstances, they remain electrically silent. All other inspiratory rib cage muscles only insert on the pulmonary rib cage.

Probably the most important expiratory rib cage muscle is the triangularis sterni muscle, which originates from the lateral border of the sternum and runs axially and laterally in a cephalad direction to insert into the lower border of the ribs of the pulmonary rib cage.8

The abdominal rib cage is exposed on its inner surface to \( P_{ab} \) over the surface of the diaphragm. This pressure, in contrast to \( P_{pl} \) over the surface of the lung, generally rises during inspiration. This reflects the rise in abdominal pressure (\( P_{ab} \)) when the diaphragm contracts and pushes down on the abdominal contents, displacing the abdomen outward. \( P_{ab} \) is transmitted through the costal diaphragmatic fibers to the pleural space in the area of apposition and acts to expand the abdominal rib cage.13 In addition, the costal diaphragmatic fibers originate from ribs 7 to 11 and run axially in the area of apposition to insert on the central tendon. Thus, with diaphragmatic contraction there is a cephalad force acting on the abdominal rib cage in concert with \( P_{ab} \) to expand it.15,16 The abdominal muscles are also attached to the abdominal rib cage, and when they are recruited, they act to contract it.3

Apart from a small slip of the costal part of the diaphragm attached to the sternum, the diaphragm has no attachments on the pulmonary rib cage and therefore has no direct action on it. Therefore, to a reasonable approximation, the agencies acting on the pulmonary rib cage in the absence of rib cage distortion are \( P_{pl} \) over the surface of the lung and the pressures developed by the rib cage muscles (\( P_{n.m} \)). At equilibrium, these agencies must be balanced by the elastic recoil pressure of the pulmonary rib cage (\( P_{rcm} \)): \( P_{n.p} = P_{n.m} + P_{pl} \). In contrast, the agencies acting on the abdominal rib cage in the absence of rib cage distortion are \( P_{ab} \), a fraction of transdiaphragmatic pressure (\( P_{di} = P_{ab} - P_{pl} \)), called the insertion component of \( P_{di} \) (\( xP_{di} \), where \( 1 \geq x \geq 0 \)),15–17 and a fraction of the pressure developed by the abdominal muscles (\( P_{abm} \)), called the insertional component of \( P_{abm} \) (\( yP_{abm} \), where \( 1 \geq y \geq 0 \)).17

At equilibrium, these agencies must be balanced by the elastic recoil of the abdominal rib cage (\( P_{n.a} \)): \( P_{n.a} = xP_{di} + P_{ab} - yP_{abm} \). \( yP_{abm} \) is given a negative sign because its action is deflationary, whereas \( xP_{di} \) and \( P_{ab} \) are inflationary. Although the rib cage can be easily distorted,18–20 in quiet breathing and exercise this does not occur to any significant extent.3

Therefore:

\[
P_{n.p} = P_{n.a} = P_{n.m} + P_{pl} = xP_{di} + P_{ab} - yP_{abm}
\]

and by rearranging:

\[
P_{n.m} = (x + 1)P_{di} - yP_{abm} \quad (7-1)
\]

In a similar manner to the rib cage, motion of the abdomen can be described by the motion of two subcompartments: the cephalad portion of the abdominal wall is attached to the costal margin and moves when the costal margin moves9,12, the caudal portion of the abdominal wall is not moved by the costal margin. Thus, the cephalad portion is the only part of the abdominal wall that can be pulled outward with an inspiratory action as a result of muscle contraction. But this muscular action is primarily on the rib cage, not the abdomen. No abdominal muscles act to expand the abdominal wall. Thus, the caudal part of the abdominal wall always expands passively, either as a result of an increase in abdominal pressure due to diaphragmatic contraction or because of relaxation of abdominal muscle contraction, when abdominal pressure can actually fall during abdominal expansion.17

### ACTIONS OF INDIVIDUAL RESPIRATORY MUSCLE GROUPS

Let us consider the actions of the abdominal muscles. Among them, the rectus abdominis muscle does not seem to be important for breathing. The most important is the transversus muscle, and the oblique muscles are probably both postural and respiratory.3 These muscles form the anterolateral abdominal wall and insert into the costal margin; they can therefore act on the abdominal rib cage.1,21 When they contract by themselves, they displace the abdominal wall inward, compress the abdominal contents, increase \( P_{ab} \), and passively stretch the relaxed diaphragm.

Their action on the rib cage is considerably more complex. In the upright posture, the abdominal muscles are passively stretched by gravity acting ventrally on the abdominal contents and demonstrate tonic electrical activity.3,22,23 Therefore, the abdominal muscles must have a restrictive action on the abdominal rib cage during inspiration.21 In the supine posture, on the other hand, gravity acts dorsally rather than ventrally, and the abdominal muscles are electrically silent,22,23 so that they have no action on the abdominal rib cage. This postural change in the forces acting on the rib cage has not been well studied.

When the abdominal muscles contract in isolation, they passively stretch the diaphragm. The passively stretched costal fibers exert an inflationary action on the abdominal rib cage, as does the increase in \( P_{ab} \), which is transmitted through the diaphragm to its inner surface. However, the tension transmitted from the abdominal muscles at the costal margin tends to deflate this part of the rib cage. The increase in \( P_{ab} \) is transmitted to the pleural space to increase \( P_{pl} \) but is reduced by whatever passive \( P_{di} \) is present. The increase in \( P_{pl} \) acts to inflate the pulmonary rib cage, while it deflects the lung. To a close approximation, the volume of abdominal contents is constant. The movable surfaces of the abdomen are the ventral and lateral surfaces of the abdominal wall and the diaphragm, which forms the abdomen’s cephalad boundary. Thus, the volume displaced by the cephalad displacement of the diaphragm must equal the volume swept by inward displacement of the abdominal wall. This is greater than the increase in chest wall volume due to pulmonary rib cage expansion. Thus, the actions of the abdominal muscles on both the lungs and abdomen are deflationary. They are expiratory muscles.

The forces acting on the pulmonary and abdominal parts of the rib cage during isolated abdominal muscle contraction are likely to be different, producing a distortion of the rib cage away from its relaxation configuration. To the
extent that the rib cage resists bending, there will be an interaction between the two rib cage compartments, tending to minimize distortions. Although, almost certainly, both rib cage compartments expand, the displacements and distortions between the two rib cage compartments have not yet been studied in detail.

Now let us see what happens when the inspiratory muscles of the rib cage contract in isolation. These muscles, of which the most important are the scalene muscles and parasternal muscles, also include whatever external intercostal muscles are activated during breathing and the sternocleidomastoid muscles. As pointed out above, these muscles insert almost exclusively into the pulmonary rib cage. What happens when the diaphragm, often referred to as the only muscle contracting? The diaphragm’s connections with the rib cage are all at the costal margin on ribs 7 to 12 in the abdominal rib cage (except for a tiny slip at the bottom of the sternum). Thus, it has only a minimal direct action on the pulmonary rib cage. Again, the effect on the abdominal rib cage is not straightforward, and the precise displacements and distortions have not yet been accurately measured.

What happens when the diaphragm, often referred to as the most important respiratory muscle, is the only muscle contracting? The diaphragm’s connections with the rib cage are all at the costal margin on ribs 7 to 12 in the abdominal rib cage (except for a tiny slip at the bottom of the sternum). Thus, it has only a minimal direct action on the pulmonary rib cage. When it contracts, its fibers exert a force on the central tendon, which is displaced caudally, compressing the abdominal contents, increasing $P_{ab}$, and displacing the abdominal wall outward. At the same time, the fibers originating from the costal margin exert a cephalad force on the abdominal rib cage through ribs 7 to 12, and this is augmented by the increase in $P_{ab}$ acting in the area of apposition of diaphragm to rib cage. The purpose of diaphragmatic contraction is to develop a pressure difference across the muscle, so that as $P_{ab}$ increases, $P_{pl}$ decreases, thereby inflating the lung. Thus, the action of the diaphragm on both the abdomen and the lung is purely inspiratory, but the decrease in $P_{pl}$ has an expiratory effect on the pulmonary rib cage. If the diaphragm contracts against a closed glottis, when, to a close approximation, chest wall and lung volume remain constant, the pulmonary rib cage is displaced inward as the abdomen is displaced outward. Whereas the increase in $P_{ab}$ and the tension developed in the costal fibers act to expand the abdominal rib cage, this is almost exactly counterbalanced by the expiratory displacement of the pulmonary rib cage and the resistance of the rib cage to bending, so that no net movement of the abdominal rib cage occurs, and considerable rib cage distortion takes place.

The motions occurring when the diaphragm is the only muscle contracting and air is free to flow into the lung have not yet been studied with precision, but it is likely that significant rib cage distortions would also take place. The pulmonary rib cage would be caught between the expiratory force of the fall in $P_{pl}$ acting over its whole inner surface and the inspiratory action of the expanding abdominal rib cage taking the pulmonary rib cage along with it. As most of the force developed by the diaphragm on the rib cage would go into distorting it, and only a small fraction into expanding it, this would be an inefficient way to breathe. Rib cage distortions are costly, so a good way to breathe is to avoid them altogether. As discussed above, rib cage distortions are minimal during breathing in normal subjects, even during heavy exercise.

Rib cage distortions have not been studied to any significant extent in disease, but in airways obstruction with hyperinflation, one might expect a decrease in the area of apposition, and with extreme hyperinflation, a change in the direction of force exerted by the diaphragm at the costal margin from axial to radial. If this was the case, the diaphragm would tend to deflate the abdominal rib cage, both because this part of the rib cage would now be exposed to the deflationary action of $P_{pl}$ over the surface of the lung and because of the radial direction of tension in the costal fibers acting at the costal margin.

**QUICK BREATHING AT REST**

Normally, humans breathe both at rest and during exercise, in such a way that the rib cage does not distort. The undistorted configuration of the pulmonary and abdominal rib cage compartments occurs when the pressure acting on both compartments is the same. This occurs during relaxation with all muscles relaxed and $P_{pl} = P_{ab}$. During quiet breathing at rest, equal pressures acting on both compartments require that the inspiratory rib cage muscles contract to the extent that the net inflationary pressure acting on the pulmonary rib cage is identical to the net inflationary pressure produced by the agencies acting on the abdominal rib cage. This situation is described above by Equation 7-1. The inspiratory rib cage muscles must overcome the deflationary action of the fall in $P_{pl}$ on the pulmonary rib cage and develop an inflationary pressure equal to the combined effects of the direct action of the diaphragm on the abdominal rib cage, given by $xP_{ab}$, and $P_{ab}$ acting at its inner surface, minus the deflationary pressure developed by the passively stretched abdominal muscles. The fact that the measured $P_{cm}$ is only about half of $P_{di}$ during quiet breathing suggests that $yP_{abm}$ is substantial.

**BREATHING DURING EXERCISE**

A quite different pattern of breathing emerges during exercise. As soon as exercise starts, there is an immediate
recruitment of expiratory muscles, even at zero workload. The abdominal muscles are the main ones recruited; the expiratory rib cage muscles are recruited to a lesser extent. The expiratory muscles are recruited cyclically, starting at the beginning of expiration and increasing the pressure that they develop throughout expiration, which reaches its maximal value at end-expiration. Then they do not relax right away, but slowly throughout inspiration (Figure 7-1).

This results in a $P_{ab}$ that is high at the beginning of inspiration but falls progressively throughout inspiration, in striking contrast to breathing at rest, when $P_{ab}$ increases throughout inspiration. The pressures developed by the various respiratory muscle groups during quiet breathing and as a function of exercise workload are shown in Figure 7-2. At rest, only the diaphragm and the inspiratory rib cage muscles are active. At the onset of exercise, even at zero workload, the abdominal and expiratory rib cage muscles are recruited. Surprisingly, $P_{di}$ decreases from quiet breathing to zero workload exercise, and as exercise workload increases, $P_{di}$ only increases modestly. At zero workload and above, $P_{abm}$ and $P_{rcm}$ are considerably greater than $P_{di}$.

Evidently, as soon as exercise starts, there is an immediate change in the central drive to the respiratory muscles. This drive activates the muscles to produce power, the product of the flow they generate and the pressure they produce. But how this power is partitioned between flow and pressure is not determined by the central drive; it is a unique function of the load that the muscle acts against. During breathing at rest, $P_{ab}$ rises and $P_{pl}$ falls throughout inspiration, progressively increasing the load on the diaphragm, because both pressures act to impede diaphragmatic descent. The increase in $P_{ab}$ and decrease in $P_{pl}$ represent the interaction between the activation of the diaphragm produced by the central drive and the elastic loads of the lung and chest wall that the diaphragm is acting against. For a given degree of activation, as these loads increase during inspiration, more of the central drive to the diaphragm is converted into $P_{di}$ and less is converted into flow.

Quite the opposite situation pertains during exercise. The decrease in $P_{ab}$ during inspiration shown in Figure 7-1 parallels the decrease in $P_{pl}$. If $\Delta P_{ab} = \Delta P_{pl}$, then the diaphragm would contract quasi-isotonically, and the elastic loads would disappear. Thus, the gradual relaxation of abdominal muscles throughout inspiration unloads the diaphragm so that more of the central drive is converted to flow and less to pressure. This is illustrated in Figure 7-3, which shows that most of the diaphragm's power during exercise is expressed as flow rather than pressure. Indeed, the fold increases in power developed by the inspiratory rib cage muscles, the abdominal muscles, and the diaphragm as a function of exercise workload are all about the same (Figure 7-4). The fact that inspiratory $P_{rcm}$ and $P_{abm}$ exceed $P_{di}$ indicates that the diaphragm's role during exercise is primarily as a flow generator, whereas the
inspiratory rib cage and abdominal muscles are primarily pressure generators acting to displace the rib cage and abdomen, respectively. This is shown for the diaphragm and inspiratory rib cage muscles in the lower panel of Figure 7-4, in which the power developed by these muscles is partitioned into its pressure and flow components as the ratio between pressure and velocity of shortening.

During exercise, the conditions for no rib cage distortion are the same as in Equation 7-1, except that \( P_{abm} \) is both active and passive. Expressing Equation 7-1 in terms of changes gives:

\[
\Delta P_{rcm} = (x + 1) \Delta P_{di} - y \Delta P_{abm} \tag{7-2}
\]

\( P_{rcm} \) now includes both inspiratory and expiratory rib cage muscles. The condition for both lack of rib cage distortion and isotonic diaphragm contraction is obtained by setting \( \Delta P_{di} = 0 \) in Equation 7-2:

\[
P_{rcm} = -yP_{abm} \tag{7-3}
\]

Equation 7-3 states that a simple control system by which the central drive to the combined inspiratory and expiratory rib cage muscles is exactly 180° out of phase with the drive to the abdominal muscles, with a constant of proportionality equal to \( y \), accomplishes two remarkable things: it prevents costly rib cage distortions and removes the elastic load from the diaphragm, allowing it to act as a flow generator. The plot of \( P_{rcm} \) versus \( P_{abm} \) during exercise is shown in Figure 7-5 and confirms that the pressures developed by these two muscle groups are, in fact, nearly 180° out of phase.

In addition to preventing rib cage distortions and allowing the diaphragm to act as a flow generator, the
abdominal muscles play another important role: end-expiratory lung volume progressively decreases as exercise workload increases. This allows elastic energy to be stored in the system below FRC that can be released to perform useful external work during inspiration. Furthermore, the reduction in end-expiratory lung volume is entirely accomplished by a reduction in the volume of the abdominal compartment; there is no decrease in the volume of the rib cage at end-expiration, whereas all the increase in lung volume takes place in the rib cage compartment. This is shown in Figure 7-6. As the volume of the abdomen is the main determinant of diaphragmatic fiber length,\(^\text{25}\) its inward displacement lengthens the diaphragm fibers, allowing it to generate more power for a given degree of central activation.

**SUMMARY AND CONCLUSIONS**

There are three sets of respiratory muscles, namely the diaphragm, the abdominal muscles, and the rib cage muscles. Each has a unique action on the three compartments comprising the chest wall, namely the pulmonary or lung-apposed rib cage, the abdominal or diaphragm-apposed rib cage, and the abdomen. Although it is possible to breathe with only one of these three, isolated contraction of each has unwanted effects on at least one of the compartments. To prevent these effects, coordinated recruitment of two or three sets of muscles is required. During breathing at rest, this is accomplished by the coordinated activity of the diaphragm and inspiratory rib cage muscles. Normally, no expiratory muscles are used. During exercise, the abdominal muscles, and to a lesser extent the expiratory rib cage muscles, are immediately recruited. The abdominal muscles, in concert with the rib cage muscles, play a double role of preventing costly rib cage distortions and unloading the diaphragm so that it acts as a flow generator, whereas the rib cage and abdominal muscles take on the task of developing the pressures required to move the rib cage and abdomen, respectively. The abdominal muscles play a third role in decreasing end-expiratory lung volume by decreasing the volume of the abdomen. This stores elastic energy in the respiratory system that can be released during inspiration to perform useful external work. It also lengthens diaphragmatic fibers so that they develop more power for a given level of activation.

**REFERENCES**


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**FIGURE 7-6** Volume changes of the lung-apposed rib cage \(V_{rc,p}\), the diaphragm-apposed rib cage \(V_{rc,a}\), and the abdomen \(V_{ab}\) during quiet breathing and as a function of exercise workload. On the ordinate, the volumes are referenced to functional residual capacity (FRC) during quiet breathing (0.0). Open circles: end-inspiratory volume; closed circles: end-expiratory volume. Reproduced with permission from Aliverti A et al.\(^\text{17}\).