The two mechanisms of intercostal muscle action on the lung

Theodore A. Wilson\(^1\) and Andre De Troyer\(^2\)

\(^1\)Department of Aerospace Engineering and Mechanics, University of Minnesota, Minneapolis, Minnesota 55455; and \(^2\)Laboratory of Cardiorespiratory Physiology, Brussels School of Medicine, Erasme University Hospital, 1070 Brussels, Belgium

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Wilson, Theodore A., and Andre De Troyer. The two mechanisms of intercostal muscle action on the lung. J Appl Physiol 96: 483–488, 2004; 10.1152/japplphysiol.00553.2003.—The mechanisms of respiratory action of the intercostal muscles were studied by measuring the effect of external forces (F) applied to the ribs and by modeling the effect of F exerted by the intercostal muscles. In five dogs, with the airway occluded, cranial F were applied to individual rib pairs, from the 2nd to the 11th rib pair, and the change in airway opening pressure (Pao) was measured. The ratio Pao/F increases with increasing rib number in the upper ribs (2nd to 5th) and decreases in the lower ribs (5th to 11th). These data were incorporated into a model for the geometry of the ribs and intercostal muscles, and Pao/F was calculated from the model. For interspaces 2–8, the calculated values agree reasonably well with previously measured values. From the modeling, two mechanisms of intercostal muscle action are identified. One is the well-known Hamberger mechanism, modified to account for the three-dimensional geometry of the rib cage. This mechanism depends on the slant of an intercostal muscle relative to the ribs and on the resulting difference between the moments applied to the upper and lower ribs that bound each interspace. The second is a new mechanism that depends on the difference between the values of Pao/F for the upper and lower ribs.

rib-lung coupling; mechanical advantage; Hamberger; dog

THE BONES OF THE RIB CAGE are interconnected by joints and cartilage. The displacements of the ribs (Xr) are constrained by these connections, and forces (F) that are applied to the ribs by an intercostal muscle are transmitted through the joints and cartilage to other bones. As a result, the relation between muscle F and bone displacement for the intercostal muscles is more complicated than it is for most skeletal muscles. For example, for the inspiratory muscles, muscle shortening is transformed by these interconnections into expansion of the thorax. Furthermore, the quantitative relation between Xr and thoracic volume expansion and the fraction of thoracic volume expansion that is transmitted to the lungs is difficult to estimate. Moreover, it has not been possible to determine experimentally the respiratory effect of all intercostal muscles directly, because it has not been possible to selectively activate individual intercostal muscle groups. As a result of these difficulties, the respiratory action of the intercostal muscles has long been a controversial subject.

The dominant current concept of intercostal muscle action is due to Hamberger (5). According to Hamberger, the respiratory effect of an intercostal muscle is the result of the different moments (M) that the muscle exerts on the upper and lower ribs that bound an interspace. For the external intercostals, the F exerted on the upper and lower ribs are equal and opposite, but the point of attachment on the lower rib is further from the axis of rib rotation than the point of attachment on the upper rib. As a result, the M are unequal, the net M is inspiratory, and the external intercostals have an inspiratory effect. Conversely, the internal intercostals have an expiratory effect. Hamberger’s argument is based on a two-dimensional model in which the ribs are pictured as straight rods connected to the spine and linked by the sternum. Because of the constraint imposed by the sternal link, the angular rotations of both ribs are equal. Thus the Hamberger model does not include the possibility that different ribs have different rotational compliances. Also, Hamberger does not address the question of the relation between Xr and lung volume. He simply assumes that an upward rotation has an inspiratory effect and a downward rotation has an expiratory effect. Thus the model does not include the possibility that the coupling between muscle F and lung expansion is different for different ribs.

De Troyer et al. (3) have evaluated the respiratory effects of the intercostal muscles of the dog, using an indirect method. Changes in muscle length l during passive lung inflation were measured, and, from these data, the effects of active tension in the muscles were inferred by application of Maxwell’s reciprocity theorem. For a number of muscles, the parasternal intercostals in different interspaces (2, 7), the triangularis sterni (1), and the sternomastoids and scalenes (6), the predictions obtained by this indirect method have been compared with direct measurements of muscle action and found to be accurate. The results of De Troyer et al. (3) are reported as values of mechanical advantage (μ) of the muscles, where μ is defined, as stated by Eq. 1, as the change in airway opening pressure (Pao) per unit muscle mass (m) and active stress (σ) that is produced when the muscle is activated with the airway occluded

\[
\mu = \frac{\text{Pao}}{m\sigma}
\]

The sign of μ describes the qualitative effect of the muscle (negative for inspiratory effect and positive for expiratory effect), and the magnitude of μ describes the magnitude of muscle effectiveness. Some features of the results of De Troyer et al. are consistent with the Hamberger model. At most points on the chest wall, the value of μ for the external intercostal is more negative than the value of μ for the internal intercostal. Thus, at most points, the external intercostal has a more inspiratory (or less expiratory) effect than the internal intercostal. However, many features of their results are not explained by the Hamberger model. The values of μ for both the externals and internals depend strongly on location. Within

Address for reprint requests and other correspondence: T. A. Wilson, 107 Akerman Hall, 110 Union St. SE, Minneapolis, MN 55455 (E-mail: wilson@acom.umn.edu).

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each interspace, the value of \( \mu \) depends on circumferential position, and, across interspaces, the values of \( \mu \) for both externals and internals shift systematically from more inspiratory values in the cranial interspaces to expiratory values in the caudal interspaces. In fact, at the ventral end of the second interspace, the internal intercostal has an inspiratory effect, and, in the 8th and 10th interspaces, the external intercostals have expiratory effects. For these muscles, the sign of the respiratory effect is opposite that predicted by the Hamberger model.

We have also reported data on the respiratory effect of an external \( F \) applied to a rib (4). These data show that both rib compliance and the coupling between \( X_r \) and lung expansion vary with rib number. As a result, the respiratory effect of \( F \) increases with increasing rib number for the more cranial ribs and then decreases with increasing rib number for the more caudal ribs. We noted that this nonuniformity could explain the dependence of \( \mu \) on interspace number.

Here, we report data from more systematic measurements of the respiratory effect of external \( F \) applied to the ribs. In these experiments, \( F \) in the cranial direction were applied to the left and right ribs of each pair rib with the airway occluded, and the change in airway pressure was measured. To account for the fact that the intercostal muscles are distributed around the circumference of the rib cage and exert \( F \) in different directions, a model for the geometry of the ribs and muscles was formulated. With this model, the experimental data were transformed into predictions of the mechanical advantage of the intercostal muscles.

Comparison between the values of mechanical advantage predicted from the model and the earlier experimental values (3) provides a quantitative test of our understanding of intercostal muscle action. For interspaces 2–8, the predicted values agree reasonably well with the experimental values. From the model, two mechanisms of intercostal muscle action are identified, and the contributions of each mechanism to the total respiratory effect of different muscles are obtained.

**METHODS**

The studies were approved by the Animal Ethics and Welfare Committee of the Brussels School of Medicine. Five adult mongrel dogs (11–18 kg body mass) were anesthetized with pentobarbital sodium (initial dose, 30 mg/kg iv) and placed in the supine posture. The animal was intubated with a cuffed endotracheal tube, and a differential pressure transducer (Validyne, Northridge, CA) was connected to a side port of the endotracheal tube to measure \( P_{ao} \). A venous cannula was inserted in the forelimb to give maintenance doses of anesthetic (3–5 mg·kg\(^{-1}\)·h\(^{-1}\) iv), and a cannula was inserted in the right femoral artery to monitor blood pressure and heart rate. The rib cage and intercostal muscles were exposed on both sides of the chest from the 1st to the 12th rib by deflection of the skin and the superficial muscle layers, and hooks were screwed into the second left and right bony ribs, 1–2 cm lateral to the costochondral junctions. A string was attached to each hook and led cranially over a pulley to a small basket in which weights could be placed. An additional hook was screwed into the second rib at the midaxillary line and connected to a linear displacement transducer (Schaevitz Engineering, Pennsauken, NJ) to measure the cranial \( X_r \). After instrumentation, the animal was allowed to recover for 15 min.

The animal was then paralyzed with an intravenous injection of 2 mg pancuronium and ventilated mechanically. After calibration of the displacement transducer, ventilation was stopped, and the chest wall was allowed to relax to equilibrium. The endotracheal tube was occluded, 0.2-kg steel balls were placed in both baskets attached to the second rib pair, and \( P_{ao} \) and \( X_r \) were recorded. The load in each basket was increased by 0.2-kg increments to 0.6 kg. The load was removed, and the incremental loading procedure was repeated. The hook basket system and the displacement transducer were transferred to the third rib pair, and pressure and \( X_r \) for two runs of incremental loading were obtained. The procedure was repeated for each rib pair down to the 11th rib pair.

No changes in blood pressure or heart rate occurred during the course of the experiments. The pupils in each animal remained consstricted and unresponsive to light, indicating a deep level of anesthesia. At the end of the experiment, the animal was given an overdose (30–40 mg/kg) of anesthetic.

**Data analysis.** For each rib pair in each animal, values of \( P_{ao} \) and \( X_r \) for each \( F \) for the two runs were averaged. The slopes (\( P_{ao}/F \) and \( X_r/F \)) of lines fit to the data were obtained. The values of \( r^2 \) for these fits for ribs 2–8 ranged from 0.984 to 0.998. The values of \( r^2 \) for ribs 10 and 11 were lower. Values of \( P_{ao}/X_r \) were obtained as the ratio of \( P_{ao}/F \) to \( X_r/F \). The values \( P_{ao}/F, X_r/F \), and \( P_{ao}/X_r \) for each rib were averaged over the five animals, and these averages \( \pm \) SE are reported.

**EXPERIMENTAL RESULTS**

The average values (\( \pm \) SE) of \( X_r/F, P_{ao}/F, \) and \( P_{ao}/X_r \) for the five animals are shown plotted vs. rib number in Figs. 1, 2, and 3, respectively. \( X_r/F \) increases progressively from the second to ninth rib. The magnitudes of \( P_{ao}/F \) and \( P_{ao}/X_r \) increase from the second to the fifth rib and then decrease with increasing rib number.

**Model.** The model for the geometry of the ribs and intercostal muscles is shown in Fig. 4. Each rib is represented as a circular arc with radius \( R \), and each rib rotates around an axis that lies in the plane of the rib and is inclined to the sagittal midplane by the angle \( \psi \) (Fig. 4A). A perspective view of the \( n \)th and \((n + 1)\)th ribs that bound the \( n \)th interspace is shown in Fig. 4B. The planes of the ribs are perpendicular to the \( z \) direction, and the distance between the planes of the ribs is...
denoted \( a \). An intercostal muscle that is inclined from the \( z \) direction by the angle \( \theta \) is shown. The points of attachment of the muscle to the \( n \)th and \((n + 1)\)th ribs are described by the angles, \( \theta_n \) and \( \theta_{n+1} \), respectively.

An \( F \) in the \( z \) direction applied to a rib produces a \( M \) about the axis of rotation of the rib and, with the airway occluded, causes a change in \( Pao \). To start the analysis of the action of the intercostals, the relation between \( Pao \) and \( M \) is written in the following trivial form

\[
Pao = M(Pao/M) 
\]

In the experiments, the external \( F \) was applied at a point at which the moment arm around the axis is approximately equal to its maximum value, \( R \). Thus \( M = RF \) and \( (Pao/M) = (1/R) \) [(\( Pao/F \))\textsubscript{exp}], where \( (Pao/F)\textsubscript{exp} \) denotes the measured values of \( Pao/F \). Substituting this expression into Eq. 2 yields the following equation

\[
Pao = (M/R)(Pao/F)\textsubscript{exp} \quad (3)
\]

Equation 3 describes the effect of any \( M \) applied to the rib. Thus this equation can be used to analyze the effect of the \( M \) applied by an intercostal muscle. An intercostal muscle applies equal and opposite \( F \) to the two ribs that bound the interspace, and the \( M \) that are applied to the two ribs are opposite in sign but different in magnitude. The net value of \( Pao \) that results from the \( M \) exerted on both ribs, denoted \( Pao_m \), equals the difference between the magnitudes of the values of the \( Pao \) for the two ribs. The expression for \( Pao \) given by Eq. 3 has the form \( z = xy \). For small differences \( \delta \) in the factors \( x \) and \( y \), the difference in \( z \) is given by \( y\delta x + x\delta y \). Thus, to a good approximation, the net effect produced by an \( F \) in an intercostal muscle is given by Eq. 4.
\[ \text{Pao}_m = [(\text{Pao/F})_{\text{exp}}] \delta(M/R) + (M/R) \delta[(\text{Pao/F})_{\text{exp}}] \]  (4)

where \( \delta(M/R) \) is the difference between the magnitudes of \( M/R \) for the \( (n + 1) \)th and \( n \)th ribs, \( \delta[(\text{Pao/F})_{\text{exp}}] \) is the difference between the values of \( (\text{Pao/F})_{\text{exp}} \) for the two ribs, and overbars denote the average values for the two ribs. From the definition of \( \mu \), given by Eq. 1, it follows that \( \mu \) is given by the following equation

\[ \mu = [(\text{Pao/F})_{\text{exp}}] \delta(M/\sigma M R) + (M/\sigma M R) \delta[(\text{Pao/F})_{\text{exp}}] \]  (5)

In the following development, the first term on the right side of Eq. 5 is denoted \( A \), and the second is denoted \( B \).

The \( M \) on the rib due to active muscle \( F \) \( (F_m) \) is the product of the component of the \( F \) in the direction perpendicular to the plane of the rib and the perpendicular distance from the axis of rotation to the point of attachment of the muscle. It can be seen from inspection of Fig. 4 that the component of \( F_m \) in the direction perpendicular to the plane of the rib is \( F_m(a/l) \) and that the perpendicular distance between the axis of rotation and the point of attachment is \( R \sin(\theta - \psi) \). Thus \( M/R = F_m(a/l) \sin(\theta - \psi) \). The difference between the values of \( M/R \) for the two ribs is the result of the difference in the values of \( \theta \). Thus \( \delta(M/R) = F_m(a/l) \cos(\theta - \psi) \delta \theta \), and again by inspection of Fig. 4, \( \delta \theta \approx -(l/R) \sin \phi \). The active \( F \) carried by the muscle is the product of \( \sigma \) and cross-sectional area \( S \). Because the density of muscle is \( \sim 1 \text{ g/cm}^3 \), the numerical value of \( m \) in grams approximately equals the numerical value of muscle volume in cubic centimeters. Therefore, \( m \) is the product of \( S \) and muscle \( l \), where \( l = [a^2 + (R_n + R_{n+1})^2]^{1/2} / \cos \phi \). With these substitutions, the model equations for \( \mu \) take the following form

\[ \mu = A + B \]  (6)

\[ A = -a \frac{\sin \phi \cos(\theta - \psi)}{lR} [(\text{Pao/F})_{\text{exp}}] \]  (7)

\[ B = a \frac{\sin(\theta - \psi)}{l} \delta[(\text{Pao/F})_{\text{exp}}] \]  (8)

where

\[ l = [a^2 + (R_{n+1} - R_n)^2]^{1/2} / \cos \phi \]  (9)

where \( \theta \) is the average angular position of the muscle.

Calculations of \( \mu \) and comparisons with experimental values. The expressions for \( A \) and \( B \) were evaluated as functions of \( \theta \) for interspaces 2, 4, 6, and 8. The values of \( R \) and \( a \) that were used in these calculations are listed in Table 1. The values of \( R \) are the average of the major and minor radii of ellipses fit to rib data by Margulies et al. (8), scaled by a factor of 1.05 to account for the fact that the masses of the dogs used by Margulies et al. were smaller than those of the dogs used in the present study. The values of \( a \) were also obtained from the report of Margulies et al. and scaled by the same factor. The values \( \psi = 20^\circ \) and \( \phi = -40^\circ \) and 50° for the external and internal intercostals, respectively, were used for all interspaces.

The calculated values of \( A \) and \( B \) for interspaces 2 and 6 are shown in Fig. 5. Term \( A \) is proportional to \( \sin \phi \), and thus its sign depends on the sign of \( \phi \). In all interspaces, the sign is negative (inspiratory) for the external intercostals and positive (expiratory) for the internal intercostals. The magnitude of \( A \) is maximum at the dorsal end of the interspace and zero at \( \theta = \psi + 90^\circ \). The sign of \( B \) depends on the sign of the difference between the values of \( (\text{Pao/F})_{\text{exp}} \) for the lower and upper ribs. Thus, for both the external and internal intercostals, the sign is negative in interspace 2 and positive in interspace 6. The magnitude of \( B \) is zero at the dorsal end of the interspace and maximum at \( \theta = \psi + 90^\circ \).

In Fig. 6, the calculated values of \( \mu \) for interspaces 2, 4, 6, and 8 are compared with the experimental values previously obtained by De Troyer et al. (3). The latter values were scaled because the dogs used in those experiments (3) were bigger than the dogs used in the experiments reported here. Because both the pressures generated by the respiratory muscles and the magnitude of the \( a \) in muscle are roughly independent of animal size, but muscle mass is roughly proportional to body mass, \( \mu \) would be expected to be inversely proportional to animal mass. Therefore, the values of \( \mu \) reported by De Troyer et al. (3) were multiplied by 3/2, the ratio of the average body mass of the dogs used in the earlier experiments to the average body mass of the dogs used in the present experiments. In general, the agreement between the calculated values of \( \mu \) and the previously measured values is good.
increases for the cranial ribs and then remains about constant (8). Thus the greater displacement per unit F may be the result of a greater $M$ per unit F on the more caudal ribs. $Pao/Xr$ increases from the 2nd to the 5th rib and then decreases markedly from the 5th to the 11th rib. Again, the increase with increasing rib number in the more cranial ribs may simply be the result of increasing rib $R$: the bigger the $R$, the bigger the volume swept for a given displacement. However, the marked decrease for the caudal ribs seems to imply a change in the relation between $Xr$ and $Pao$. In the earlier paper (4), we hypothesized that this decrease is due to the fact that displacements of the more cranial ribs produce a volume expansion of the region of the rib cage directly apposed to the lung, whereas displacements of the more caudal ribs produce a volume expansion of a region of the rib cage that is at least partially apposed to the abdomen. Because the diaphragm forms an elastic partition between the abdomen and lung, volume displacements applied directly to the lung have a larger effect on $Pao$ than volume expansions applied to the abdomen, which must be transmitted through the diaphragm to affect $Pao$. The shape of the plot of $Pao/Xr$ vs. rib number is crucial: the peak in this curve produces the peak in the plot of $Pao/F$ vs. rib number.

The data for $Pao/F$ shown in Fig. 2 describe the respiratory effect per unit cranial F applied to the rib. $Pao/F$ increases from the 2nd to 5th rib and decreases from the 5th to 11th rib. This dependence of $Pao/F$ on rib number implies that the effect of a cranial F applied to the lower rib of an interspace would not be balanced by the effect of an equal and opposite F applied to the upper rib. For interspaces 2–4, the net respiratory effect of equal and opposite F would be inspiratory, and, for interspaces 5–10, the net effect would be expiratory.

To use the data on $Pao/F$ to infer values of the net respiratory effects of F applied to adjacent ribs by intercostal muscles, a model for the geometry of the ribs and muscles was formulated. This model, shown in Fig. 4, is simplified. In reality, the ribs of the dog are not circular, and the orientations of the planes of the ribs change with rib number. Also, the values that we chose for the parameters of the model are approximate. The data on which they are based were obtained from different dogs that were different breeds and different sizes. In particular, the position of the axis of rotation of the rib is not well established. However, we think that the simple model contains the main geometric features of the rib cage that affect intercostal muscle action, and, with these simplifications, transparent algebraic expressions for $\mu$, Eqs. 6–8, are obtained.

Term A in the equation for $\mu$ describes the effect of the difference in the $M$ applied to the upper and lower ribs that bound an interspace because of the difference in the circumferential positions of the points of attachment of the muscle on the two ribs. Thus the mechanism that this term describes is the same as that in the Hamberger model. Hamberger’s model, however, was two-dimensional, and, in a two-dimensional model, the respiratory effect of a muscle is independent of the location of the muscle along the rib. Our model is three-dimensional, and, as a result, the magnitude of the effect of this mechanism depends on the location of the muscle. Thus term A represents the Hamberger mechanism, modified by the three-dimensional geometry of the ribs. Term B describes the effect of a difference between the rib-lung coupling of adjacent ribs. The mechanism that this term describes is not included in the

**DISCUSSION**

Measured values (3) of the respiratory effect of the intercostal muscles are not consistent with the Hamberger description of the mechanism of intercostal action. Here, we report data on an aspect of intercostal action that is missing from the Hamberger model; namely, the coupling between the F applied to a rib and the lung. These data confirm our previous observations on the magnitude of this coupling and its dependence on rib number (4). We also present a model that incorporates these data into a description of intercostal muscle action.

In the experiments reported here, a cranial F was applied to each rib pair, and the $Xr$ and respiratory effect ($Pao$) were measured. The data for the three ratios, $Xr/F$, $Pao/F$, and $Pao/Xr$ are shown in Figs. 1, 2, and 3, respectively. These three ratios are not independent: the third is the ratio of the second to the first. Also, the three are not equally significant: $Pao/F$ contains the information about the functional effect of the F. However, $Xr/F$ and $Pao/Xr$ provide information that helps in understanding $Pao/F$.

The axial compliance (ratio of axial displacement to axial F, $Xr/F$) of each rib is described by the data shown in Fig. 1. This compliance increases with increasing rib number for the cranial ribs and is about uniform for the more caudal ribs. Rib $R$ also

![Image](http://jap.physiology.org/Download/fig-fi.png)
Hamberger model. The magnitude of Pao/F is crucial for both mechanisms. The Hamberger mechanism is proportional to Pao/F, and the second mechanism is proportional to the difference in Pao/F for adjacent ribs.

Although the model is approximate, for interspaces 2–8, the values of µ obtained from the model and the data for Pao/F agree reasonably well with the values obtained from earlier experiments (3). The Hamberger mechanism accounts for most of the difference between the respiratory effects of the external and internal intercostals in all interspaces. This difference is maximum at the dorsal end of the interspace and small at the ventral end. The second mechanism accounts for most of the dependence of the respiratory effects of both muscle groups on interspace number. That is, because the magnitude of Pao/F for rib 3 is greater than that for rib 2, the respiratory effects of both muscle groups in the second interspace have an inspiratory bias. The magnitudes of Pao/F for muscle groups in the 10th interspace have an expiratory bias. For that interspace, the calculated values of Pao/F for ribs 4 and 5 are about the same, and the second mechanism has little effect in interspace 4. From rib 5 to higher number ribs, the magnitude of Pao/F decreases, and, as a result, the respiratory effects of both muscle groups in the more caudal interspaces have an expiratory bias.

The agreement between the calculated value of µ for the dorsal portion of the internal intercostal in the eighth interspace and the measured value is poor. The calculated and measured values of µ for the 10th interspace are not shown; they are markedly different. For that interspace, the calculated values are small because the average magnitude of Pao/F is small and because the difference between the magnitudes for adjacent ribs is also small, whereas the measured values of µ for both muscle groups in the 10th interspace are large. We can think of two possible explanations for this failure of our modeling in the more caudal interspaces. First, although the geometry of these ribs has not been described quantitatively, it is apparent that it is different from the geometry of the model. The planes of the most caudal ribs are more strongly slanted in both the ventral and lateral directions than those of the more cranial ribs (8). Second, the discrepancy may be the result of a volume dependence of µ. The measured values of µ were obtained from data on change in muscle l for an increase in lung volume of 1 liter above functional residual capacity (FRC). Therefore, these are average values for the volume range from FRC to about total lung capacity. In contrast, the values of Pao/F reported here were measured at FRC. As we pointed out above and in the earlier paper (4), the lower values of Pao/F for the more caudal ribs may be the result of the fact that the more caudal ribs are partially apposed to the abdomen rather than the lung. At higher lung volume, the diaphragm is lower, the lung-apposed portion of the more caudal ribs is greater, and the values of Pao/F for these ribs may be higher than their values at FRC.

In summary, the data on Pao/F in the dog and the modeling of intercostal muscle geometry reported here yield a quantitative description of the respiratory action of the intercostal muscles. For interspaces 2–8, the values of µ calculated from the model agree reasonably well with earlier experimental values (3). Thus, for these interspaces, the respiratory action of the intercostal muscles appears to be well understood, and we conclude that, for the muscles in these interspaces, the respiratory action is the result of two mechanisms. One is the Hamberger mechanism, modified to account for the three-dimensional geometry of the ribs. The Hamberger mechanism depends on the difference between the M applied to the upper and lower ribs that bound an interspace. This mechanism accounts for the difference between the actions of the external and internal intercostals, and its magnitude is greatest near the dorsal end of the interspace. The second mechanism depends on the difference in rib-lung coupling between the upper and lower ribs. This mechanism accounts for the cranio-caudal gradient of intercostal muscle action, and its magnitude is greatest at the more ventral end of the interspace. For the dorsal portion of the internal intercostal in the 8th interspace and both intercostal muscle groups in the 10th interspace, the agreement between the calculated and measured values of µ is poor. At this point, the mechanisms of action of these muscle groups are undetermined.

The methods that were used to obtain values of µ and Pao/F in dogs cannot be used in humans. However, Wilson et al. (9) used data from computed tomography scans to determine the configuratons and locations of human ribs at FRC and total lung capacity, and, from these, they computed changes in muscle l and values of µ for the human intercostals. Although the orientations and angular rotations of human and canine ribs are different, some features of the dependence of µ on circumferential position and interspace number are similar. Specifically, in the second and fourth interspaces, the difference between the values of µ for the external and internal intercostals is greater in the dorsal region than in the ventral region. Also, in the ventral region, the values of µ for both the external and internal intercostals shift from more inspiratory values in the upper interspaces to more expiratory values in the lower interspaces. It appears, therefore, that, as in the dog, the respiratory effects of the intercostal muscles in humans are determined by both the Hamberger mechanism and the differential coupling between the ribs and the lungs.

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