

Mechanism of the increased rib cage expansion produced by the diaphragm with abdominal support

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De Troyer A, Wilson TA. Mechanism of the increased rib cage expansion produced by the diaphragm with abdominal support. *J Appl Physiol* 118: 989–995, 2015. First published February 12, 2015; doi:10.1152/jappphysiol.00016.2015.—When the abdomen in quadriplegic subjects is given a passive mechanical support, the expansion of the lower rib cage during inspiration is greater and the inward displacement of the upper rib cage is smaller. These changes have traditionally been attributed to an increase in the appositional force of the diaphragm, but the mechanisms have not been assessed. In this study, the inspiratory intercostal muscles in all interspaces were severed in anesthetized dogs, so that the diaphragm was the only muscle active during inspiration, and the displacements of the ribs 10 and 5 and the changes in pleural and abdominal pressure were measured during unimpeded breathing and during breathing with a plate applied on the ventral abdominal wall. In addition, external forces were applied to the 10th rib pair in the cranial and lateral directions, and the rib trajectories thus obtained were used as the basis for a vector analysis to estimate the relative contributions of the insertional and appositional forces to the rib 10 displacements during breathing. Application of the abdominal plate caused a marked increase in the inspiratory cranial and outward displacement of rib 10 and a decrease in the inspiratory caudal displacement of rib 5. Analysis of the results showed, however, that 1) the insertional and appositional forces contributed nearly equally to the increased inspiratory displacement of rib 10 and 2) the decrease in the expiratory displacement of rib 5 was the result of both the greater displacement of the lower ribs and the decrease in pleural pressure.

mechanics of diaphragm; insertional force; appositional force; abdominal elastance

MEASUREMENTS OF THORACOABDOMINAL motion in subjects with quadriplegia due to traumatic transection of the cervical cord have established that the diaphragm acting alone during breathing in humans produces an inward displacement of the upper portion of the rib cage and an expansion of the lower portion of the rib cage (4, 13, 17, 20, 21). Similarly, in dogs, isolated contraction of the diaphragm during inspiration displaces the upper ribs in the caudal direction and the lower ribs in the cranial and outward direction (5, 6). The expiratory action of the diaphragm on the upper rib cage is primarily caused by the fall in pleural pressure, and its inspiratory action on the lower rib cage is the result of two components of the force developed by the muscle (7). The first component, the so-called “insertional force,” is the direct cranial force applied by the muscle fibers of the costal portion of the diaphragm at the level of their insertions into the lower ribs. The second component, denoted

the “appositional force,” is the lateral force due to the transmission of abdominal pressure on the lower rib cage through the diaphragm in the zone of apposition (16).

The magnitude of the rib cage displacements produced by the diaphragm in quadriplegic subjects, however, is affected by the elastance of the abdomen and by abdominal pressure. Specifically, when the abdomen in these subjects is given a passive mechanical support by a pneumatic cuff or an elastic binder, the expansion of the lower rib cage during inspiration is increased and the inward displacement of the upper rib cage is reduced (4, 20, 21). This effect of abdominal support has traditionally been considered to be the result of an increase in the appositional force of the diaphragm. Indeed, because such a support produces an increase in abdominal pressure, the zone of apposition at end-expiration is increased. Moreover, abdominal support also causes an increase in the elastance of the abdomen. Consequently, the descent of the dome of the diaphragm in response to a given muscle activation is decreased, the zone of apposition is larger throughout inspiration, and the rise in abdominal pressure is greater. It would be expected, therefore, that the appositional force would be greater.

The role of the appositional force in facilitating the inspiratory action of the diaphragm on the rib cage in the presence of abdominal support, however, has not been assessed. Furthermore, recent studies of the mechanics of the canine diaphragm have shown that during unimpeded breathing, the insertional force contributes about half the inspiratory effect of the muscle on the lower ribs (22). These studies have also shown that, although the action of the diaphragm on the upper ribs is primarily determined by the fall in pleural pressure, the displacement of these ribs is also determined by the displacement of the lower ribs (6). Because a cuff or a binder around the abdomen causes an expansion of the zone of apposition and opposes the descent of the dome, it also lengthens the diaphragm muscle fibers and opposes their shortening during inspiration. Consequently, it should allow the fibers to operate on a more advantageous portion of their length-tension curve and, thus, to exert greater force on the lower ribs. Based on these considerations, we therefore hypothesized that in the presence of an abdominal support: 1) the increase in insertional force is likely to play a major role in the greater expansion of the lower rib cage produced by the diaphragm and 2) the smaller inward displacement of the upper rib cage is partly the result of the greater expansion of the lower rib cage. The present study was designed to test these hypotheses.

METHODS

The studies were carried out on 7 adult bred-for-research dogs (23–30 kg) anesthetized with pentobarbital sodium (initial dose, 30

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mg/kg iv) as approved by the Animal Ethics and Welfare Committee of the Brussels School of Medicine. The animals were placed in the supine position and intubated with a cuffed endotracheal tube, and a venous cannula was inserted in the forelimb to give maintenance doses of anesthetic ($3\text{--}5 \text{ mg}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ iv). The abdomen was then opened by a 4-cm-long midline incision cranial to the umbilicus, and a balloon-catheter system filled with 1.0 ml of air was placed between the stomach and the liver and connected to a differential pressure transducer (Validyne, Northridge, CA) to measure the changes in abdominal pressure (ΔPab). After the abdomen was closely sutured in two layers, the rib cage and intercostal muscles were exposed on both sides of the chest from the first to eleventh rib by reflection of the skin and superficial muscle layers, and the inspiratory intercostal muscles were eliminated from the act of breathing using the same method that has been described previously (5, 6). Thus the internal intercostal nerves in interspaces 2 to 8 on the right side and in interspaces 3 to 8 on the left side were sectioned at the chondrocostal junctions to denervate the corresponding parasternal intercostal muscles. Also, because the external intercostal nerves in the dorsal portion of the upper interspaces and the fine filaments innervating the levator costae are not readily accessible, the external intercostal and levator costae muscles in interspaces 1 to 8 were severed bilaterally from the chondrocostal junctions to the spine. The parasternal intercostal muscle in the first interspace was also sectioned bilaterally from the sternum to the chondrocostal junction. Finally hooks were screwed into the right and left 10th ribs near the midaxillary line, i.e., in one of the rib pairs into which the diaphragm inserts in the dog (14), so that the ribs could be manipulated later.

Measurements. After completion of the surgical procedure, long inextensible threads were attached to the right 5th and 10th ribs in the midaxillary line and led caudally, parallel to the longitudinal body axis of the animal, to linear displacement transducers (Schaevitz Engineering, Pennsauken, NJ) to measure the craniocaudal (axial) displacement of the upper and lower ribs, respectively. An additional thread was attached to the 10th rib and led laterally, perpendicular to the sagittal midplane of the body, to another displacement transducer to measure the laterolateral displacement of the lower ribs. This technique has been previously described in detail (8).

In addition, a balloon-catheter system filled with 0.5 ml of air was placed in the midesophagus to measure the changes in pleural pressure (ΔPpl), and a pair of silver hook electrodes spaced 3–4 mm apart was inserted in the intact parasternal intercostal muscle of the second left interspace to quantify neural inspiratory drive and to provide a time reference for pressure and rib displacement. The position of the esophageal balloon was adjusted by the occlusion technique (1), and the parasternal electrodes were implanted in parallel fibers in the muscle area known to receive the greatest neural inspiratory drive, i.e., in the vicinity of the sternum (10). The EMG signal was processed with an amplifier (model 830/1; CWE, Ardmore, PA), bandpass filtered from 100 to 2,000 Hz, and rectified before its passage through a leaky integrator with a time constant of 0.2 s.

Protocol. Baseline parameters were allowed to stabilize for 30 min after completion of the surgical instrumentation, after which measurements of rib displacements, ΔPpl , ΔPab , and parasternal intercostal EMG activity were obtained. The animal was breathing spontaneously throughout. At regular intervals, however, a custom-made wooden plate was applied on the ventral wall of the abdomen during the expiratory pause and maintained stationary for 5–6 consecutive breaths. It is worth pointing out that the placement of the plate was made so that it did not produce any rise in Pab or any displacement of the ribs at end-expiration. Also the shape of the plate was adjusted to match the shape of the epigastric region from ~ 2 cm caudal to the xiphisternum cranially to the umbilicus caudally. Presumably, therefore, the plate did not affect the length of the diaphragm at the onset of inspiration and did not impede the displacement of the lower ribs during the course of inspiration. Three to four trials of abdominal support were obtained in each animal. After the measurements were

completed, the animal was connected to a mechanical ventilator (Harvard Apparatus, Holliston, MA) and hyperventilated until the disappearance of the parasternal intercostal EMG activity.

Threads were then connected to the two hooks implanted in the 10th rib pair, and the animal was disconnected from the ventilator. While the animal was apneic, the threads were pulled gradually over a distance of 4–5 mm in two directions. First they were pulled in the direction perpendicular to the sagittal midplane of the body so as to simulate the effect of the appositional force on the rib. Next they were pulled obliquely, in the cranial-dorsal direction, to simulate the effect of the insertional force; the angle between the axis of the pull and the horizontal plane was ~ 25 degrees, in line with the orientation of the muscle fibers of the costal portion of the diaphragm in supine dogs (9, 15). Three pulls in either direction were performed in each animal.

The animals were maintained at a constant, rather deep level of anesthesia throughout the study. They had no pupillary light reflex and made no spontaneous movements other than respiratory movements during both the surgery and the measurements. The corneal reflex was also abolished during the surgery. Rectal temperature was maintained constant between 36 and 38°C with infrared lamps. At the end of the experiment, the animals were given an overdose of anesthetic (30–40 mg/kg iv).

Data analysis. The analysis of the data for each animal was made in three stages. First, phasic inspiratory electrical activity in the second left parasternal intercostal muscle during unimpeded diaphragmatic breathing (control) and during breathing with the abdominal support was quantified by measuring the peak height of the integrated EMG signal in four consecutive breaths from each trial, and the peak inspiratory displacement of rib 10 along the craniocaudal and laterolateral axes, the peak inspiratory displacement of rib 5 along the craniocaudal axis, ΔPab , and ΔPpl in the same breaths were measured relative to the onset of the parasternal inspiratory burst. Consequently, the values of rib displacement and pressure changes that were considered in the study's calculations resulted exclusively from the contraction of the diaphragm (and the single parasternal intercostal of the second left interspace) and were not corrupted by the relaxation of the abdominal and internal interosseous intercostal muscles at the end of expiration. By convention, inspiratory rib displacements in the cranial or outward direction were given positive signs. The changes in transdiaphragmatic pressure (ΔPdi) during the control breaths and during breathing with the abdominal support were also calculated ($\Delta\text{Pdi} = \Delta\text{Pab} - \Delta\text{Ppl}$).

In the second stage, the trajectories of rib 10 during the control breaths and during breathing with the abdominal support were determined by measuring the lateral rib displacement (Y) at 0.6- to 0.7-mm increments of cranial displacement (X). The values of Y were averaged over two breaths from each trial and plotted against the corresponding values of X, and the relationships were fitted by quadratic regression equations. Similarly, for each pull of the 10th rib pair in the lateral direction and the craniodorsal direction in the apneic animal, the lateral rib displacement was measured at 0.3- to 0.7-mm increments of cranial displacement, and these values were averaged over the three trials and plotted against the values of X.

As illustrated by the data obtained in a representative animal in Fig. 1A, straight lines fitted the data for rib pulling very well in every animal (coefficient of correlation, r , between 0.999 and 1.0). In agreement with our previous observation (22), however, in 6 of 7 animals, the lines of best fit did not pass through the origin. Instead, the lines had a small positive Y intercept; for the animal group, the intercept during pulling in the lateral direction was 0.15 ± 0.03 mm and that during pulling in the craniodorsal direction was 0.13 ± 0.04 mm. As previously discussed (22), these intercepts were considered to be artifacts, due to the fact that the external forces were applied at a single point on one rib, rather than being distributed around the circumference of the lower rib cage. These intercepts, therefore, were ignored, and their values were subtracted from the values of lateral rib displacement so that the relationships passed through the origin.

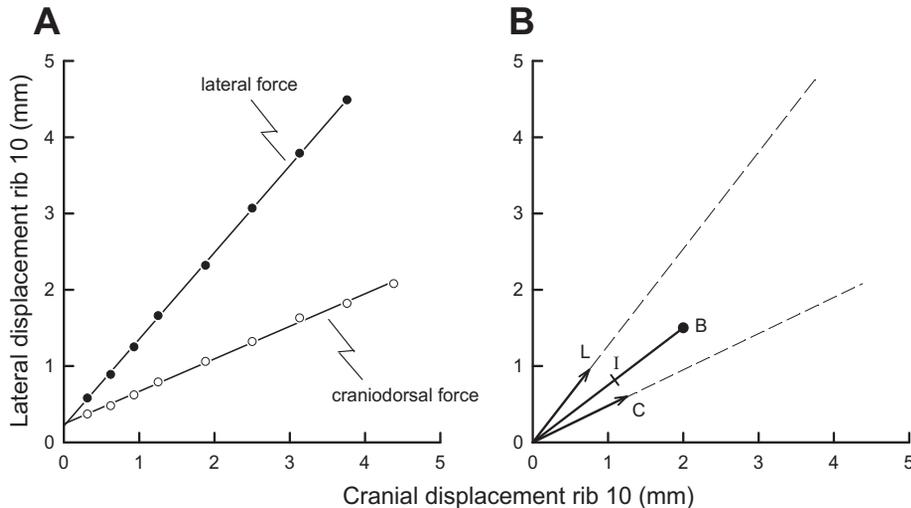


Fig. 1. A: trajectory of rib 10 during the application of external forces to the 10th rib pair in a representative animal. Lines of best fit to the data are also shown. The lines did not pass through the origin, and the small positive intercepts with the ordinate were considered to be artifacts. B: analysis of the rib 10 trajectory during breathing. Dashed lines are the relationships shown in Fig. 1A but transposed so as to pass through the origin, and the continuous line 0-B is a possible rib trajectory during spontaneous diaphragmatic breathing. See text for further explanation.

Finally, the relative contributions of the insertional and appositional components of diaphragm force to the rib 10 displacements during the control breaths and during breathing with the abdominal support were estimated by comparing the rib trajectories during breathing with those induced by external forces, as shown in Fig. 1B. The dashed lines in this panel are the rib trajectories induced by external forces in the lateral and craniodorsal directions (shown in Fig. 1A), and the solid line 0-B is a possible rib trajectory during spontaneous diaphragmatic breathing. Because this trajectory lies between the trajectories induced by external forces, the relative contributions of the two components of diaphragm force can be estimated by using a vector analysis, as previously described (22). Thus the lines 0-C and 0-L are the vectors along the external force trajectories that are the components of the resultant 0-B, and the segment 0-I is the component 0-C projected onto the resultant 0-B. The ratio of the length of the segment 0-I to the length 0-B, therefore, is the fraction of the rib displacement contributed by the insertional component, and the ratio of the length of the segment I-B to the length 0-B is the fraction of the rib displacement contributed by the appositional component. The contributions of the two components of diaphragm force would be computed similarly if the rib trajectory during breathing were curvilinear, rather than linear, but the component 0-I in this case would be the projection of the component 0-C onto the tangent to the resultant 0-B.

Data were finally averaged across the animal group, and they are presented as means \pm SE. Statistical assessment of the effects of abdominal support on rib displacements and pressure changes during diaphragmatic breathing were made by using paired *t*-tests. Statistical analysis of the trajectories of rib 10 induced by lateral vs. craniodorsal external forces and of the effect of abdominal support on the contribution of the insertional component to the displacement of rib 10 was made similarly. The criterion for statistical significance was taken as $P < 0.05$.

RESULTS

General effects of abdominal support. The records of Ppl, Pab, rib displacement, and parasternal intercostal EMG activity in the second left interspace obtained in a representative animal during control breathing and during breathing with the abdominal support are shown in Fig. 2, and the mean \pm SE values of inspiratory rib displacements and pressure changes obtained from the 7 animals are listed in Table 1. During control breathing (Fig. 2A), rib 10 moved cranially and outward during inspiration in 6 animals and was stationary in 1 animal. In

contrast, rib 5 moved caudally in all animals. For the animal group, the peak inspiratory displacement of rib 10 along the craniocaudal and laterolateral axes was $+1.09 \pm 0.25$ and $+0.82 \pm 0.19$ mm, respectively, whereas the peak inspiratory displacement of rib 5 along the craniocaudal axis was -1.00 ± 0.21 mm. These values are similar to our previous observations (5, 6, 22).

With the abdominal support (Fig. 2B), the inspiratory EMG activity recorded from the second left parasternal intercostal remained unchanged at $103.3 \pm 1.4\%$ of the control value ($0.05 < P < 0.1$), but the inspiratory cranial and outward displacement of rib 10 increased markedly in all animals ($P < 0.01$). In addition, the inspiratory caudal displacement of rib 5 was abolished in 1 animal and markedly decreased in 6 animals ($P < 0.001$). Although Δ Ppl slightly decreased relative to the control condition ($P < 0.05$), Δ Pab increased by a factor of 1.7 ($P < 0.01$). As a result, Δ Pdi was greater ($P < 0.05$).

Effect of abdominal support on rib 10 trajectories. The lateral displacements of rib 10 during control breathing and during breathing with the abdominal support are plotted against the corresponding cranial displacements for the 7 individual animals in Fig. 3. The relationship in both conditions was concave upward in one animal (*dog #2*) and that with the abdominal support was slightly concave downward in one animal (*dog #3*). In 5 of 7 animals, however, the relationships in the two conditions were linear. In fact, although the total (cranial and lateral) inspiratory rib displacement increased from 1.36 ± 0.31 mm during control to 3.65 ± 0.44 mm with the abdominal support ($P < 0.001$), the rib trajectories in the two conditions, whatever their shape, were consistently superimposed or very close to each other.

Comparison of the rib 10 trajectories during breathing with those produced by external forces. The relationships between the lateral and cranial displacement of rib 10 obtained for the 7 animals during the application of external forces on the 10th rib pair are also shown in Fig. 3. Whether the 10th rib pair was pulled in the lateral or the craniodorsal direction, rib 10 moved both cranially and outward. In every animal, however, the outward rib displacement associated with a given cranial displacement was smaller when the force was applied in the craniodorsal than the lateral direction. For the animal group as

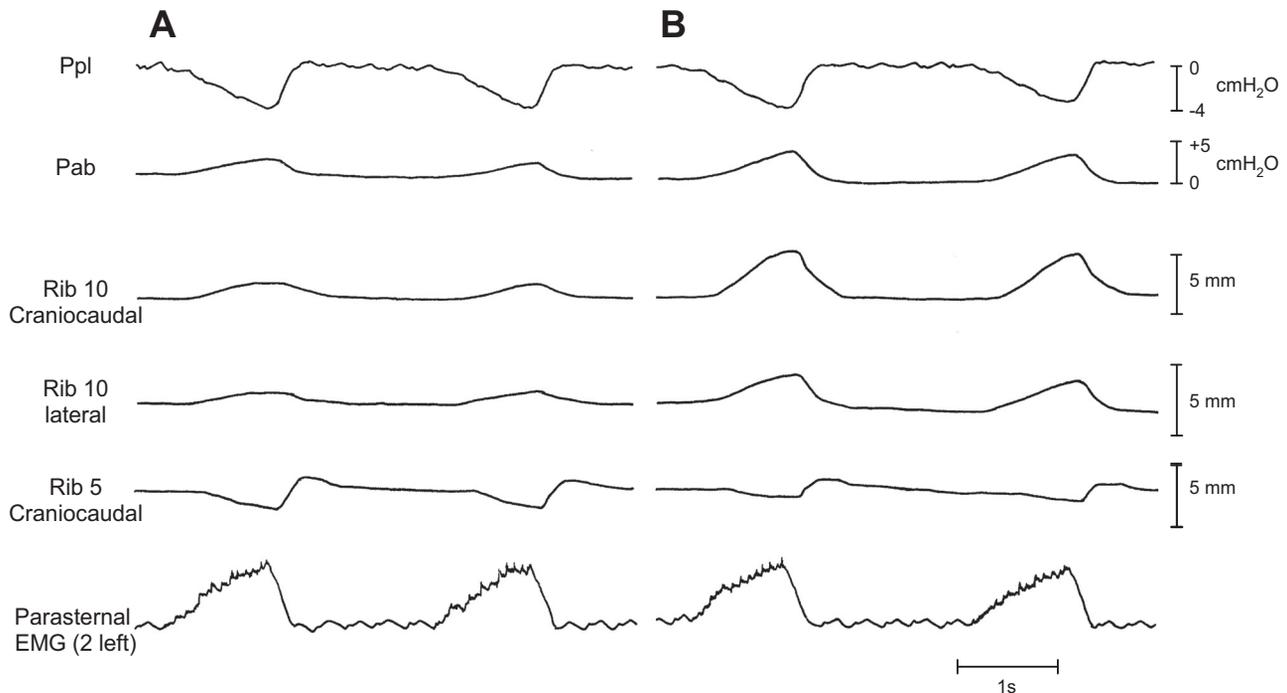


Fig. 2. Traces of pleural pressure (Ppl), abdominal pressure (Pab), and displacement of ribs 5 and 10 obtained during diaphragmatic breathing without (A) and with (B) the abdominal support in a representative animal. Trace of EMG activity in the parasternal intercostal muscle of the second left interspace is also shown as an estimate of neural inspiratory drive and a time reference. During unimpeded breathing, rib 10 was displaced in a cranial and outward direction (upward deflections) during inspiration, whereas rib 5 was displaced in the caudal direction (downward deflection). In the presence of abdominal support, Δ Pab was greater, the inspiratory cranial-outward displacement of rib 10 was markedly increased, and the caudal displacement of rib 5 was reduced. Peak EMG activity in the parasternal intercostal, however, was unchanged. Note that the application of the abdominal support did not induce any change in Pab and any displacement of the ribs at end-expiration.

a whole, the slope of the relationship between the outward and the cranial rib displacement was 1.13 ± 0.10 when the force was applied in the lateral direction, whereas with the force applied in the craniodorsal direction, the slope was only 0.56 ± 0.05 ($P < 0.001$).

As is shown in Fig. 3, the rib 10 trajectories obtained during breathing with and without the abdominal support lay between the two trajectories produced by external forces in every animal. In two animals (dogs #2 and 7), the trajectories during breathing were closer to the trajectory induced by external forces in the craniodorsal than the lateral direction, but in dog #3, the trajectories during breathing were closer to the trajectory induced by the external force in the lateral direction. The vector analysis of the data, therefore, yields the result that, for

the 6 animals that did have an inspiratory displacement of the rib during control breathing, the contribution of the insertional force to the rib 10 displacement ranged from 32 to 72% and was, on average, $56 \pm 4\%$. The computed value for the contribution of the insertional force to the rib 10 displacement during breathing with the abdominal support was similar and averaged $59 \pm 2\%$ for the 7 animals.

DISCUSSION

The application of a passive abdominal support in our animals caused a marked increase in the inspiratory cranial and outward displacement of the lower ribs and produced a decrease in the caudal displacement of the upper ribs. The EMG activity of the parasternal intercostal in the second left interspace, however, was unaltered, thus suggesting that neural drive to the diaphragm was unchanged, as previously discussed (12). These findings therefore confirm, in agreement with the effect of abdominal binding observed in quadriplegic subjects (4, 20, 21), that a mechanical support to the abdomen enhances the inspiratory action of the diaphragm on the rib cage. However, whereas the phenomenon in quadriplegic subjects has been considered to be the result of an increase in the appositional component of the force exerted by the diaphragm, the present findings suggest that the insertional component of that force and the coupling between the lower ribs and the upper ribs are equally important. In the following paragraphs, we discuss the contribution of these mechanisms to the increase in the expansion of the lower rib cage and to the decrease in the

Table 1. Effects of abdominal support on rib displacements and pressure changes during spontaneous diaphragmatic breathing

	Unimpeded Breaths	Abdominal Support
Axial motion rib 10, mm	1.09 ± 0.25	$2.91 \pm 0.34^*$
Lateral motion rib 10, mm	0.82 ± 0.19	$2.20 \pm 0.31^*$
Axial motion rib 5, mm	-1.00 ± 0.21	$-0.36 \pm 0.13^{**}$
Δ Ppl, cmH ₂ O	-4.26 ± 0.54	$-3.87 \pm 0.54 \dagger$
Δ Pab, cmH ₂ O	$+1.99 \pm 0.24$	$+3.36 \pm 0.46^*$
Δ Pdi, cmH ₂ O	$+6.24 \pm 0.70$	$+7.23 \pm 0.94 \dagger$

Values are means \pm SE for 7 animals. Δ Ppl, change in pleural pressure; Δ Pab, change in abdominal pressure; Δ Pdi, change in transdiaphragmatic pressure. $\dagger P < 0.05$, $*P < 0.01$, $**P < 0.001$ for breaths with abdominal support versus unimpeded breaths.

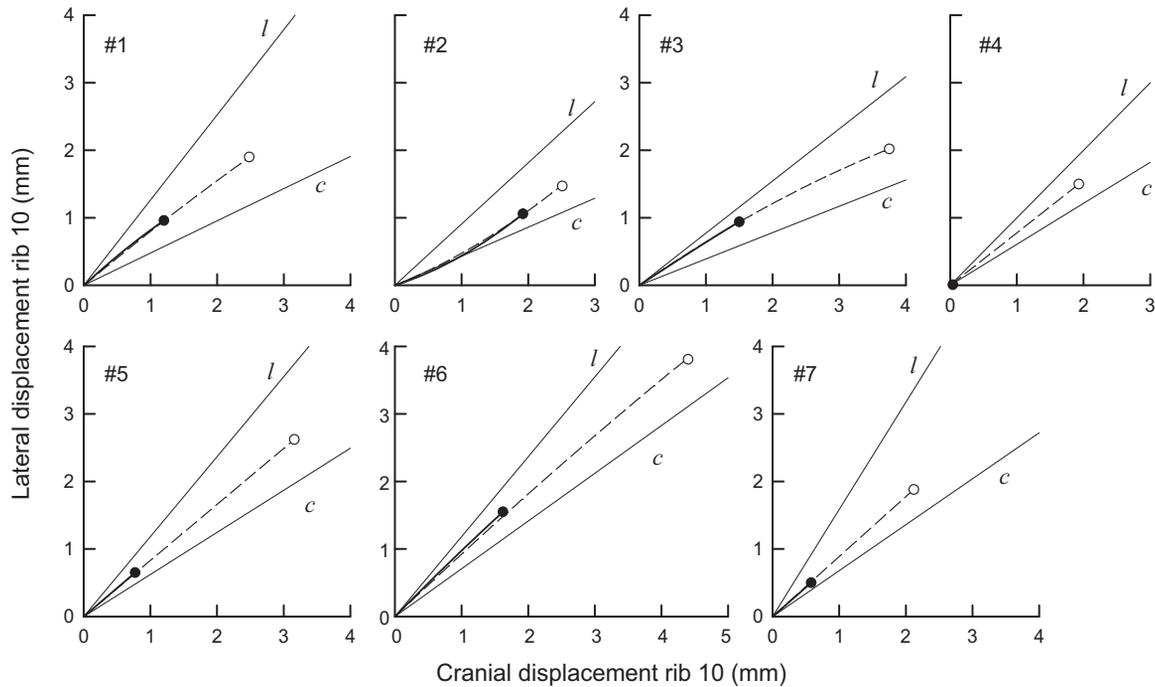


Fig. 3. Trajectories of rib 10 obtained during unimpeded diaphragmatic breathing (bold solid lines and ●), during breathing with the abdominal support (dashed lines and ○), and during the application of external forces in the lateral (thin solid line “*l*”) and craniodorsal (thin solid line “*c*”) directions in the 7 animals of the study. Note that the rib trajectories during breathing lay between the external forces trajectories in every animal. Note also that, although the cranial and outward displacement of the rib was much greater during breathing with the abdominal support than during unimpeded breathing, the rib trajectories in the two conditions were similar.

expiratory displacement of the upper rib cage produced by the diaphragm.

Mechanism of the increased expansion of the lower rib cage.

The inspiratory intercostal muscles in all but one interspace were severed in our animals, so that the diaphragm was the only muscle active during inspiration. In this condition, the only forces acting on the lower ribs are the force generated by pleural pressure and the force exerted by the diaphragm muscle fibers, which is proportional to ΔP_{di} . The displacements of the lower ribs, therefore, are functions of these variables, and this can be expressed by the following two equations, where *X* and *Y* denote the rib displacement along the craniocaudal and laterolateral axes, respectively; the coefficients *a* and *c* describe, respectively, the craniocaudal and laterolateral rib displacement produced by a unit change in ΔP_{pl} ; and the coefficients *b* and *d* describe the craniocaudal and laterolateral rib displacement produced by a unit change in ΔP_{di} :

$$X = a \Delta P_{pl} + b \Delta P_{di} \quad (1)$$

$$Y = c \Delta P_{pl} + d \Delta P_{di} \quad (2)$$

As previously pointed out (22), the only assumption embodied in these equations is that the relationships between rib displacement and ΔP_{pl} and ΔP_{di} are linear.

Two recent studies on animals of the same breed and similar size as the animals of the current study showed that the values of the coefficients *a-d* for rib 10 were, on average, *a* = 0.76, *b* = 0.72, *c* = 0.48, and *d* = 0.48 (12, 22). It would be expected that the coefficients for the animals of this study in the control condition would have nearly similar values, and indeed, with these values, substituting for ΔP_{pl} and ΔP_{di} (data shown in Table 1) in *Eqs. 1* and *2* yields the result that *X* and

Y during control breathing would be +1.25 mm and +0.95 mm, respectively. These computed rib displacements are close to the measured displacements (Table 1). If these coefficients are also used, together with the measured values of ΔP_{pl} and ΔP_{di} , for the case of abdominal support, then the predicted values for *X* and *Y* would be +2.27 mm and +1.61 mm, respectively. These computed rib displacements are substantially lower than the measured cranial (+2.91 mm) and lateral (+2.20 mm) rib displacements. Nevertheless, this result implies that the increase in ΔP_{di} , combined with the decrease in ΔP_{pl} , explains about half of the increase in the cranial and outward displacement of the lower ribs during abdominal support.

The remaining half of the increase in rib displacements, therefore, must be the result of a change in the values of the coefficients of ΔP_{pl} and ΔP_{di} in *Eqs. 1* and *2*. The plate in our animals was applied in such a way that the position of the ribs at end-expiration was unaffected. Consequently, it is reasonable to assume that the rib displacements produced by a unit change in ΔP_{pl} were unaltered and, thus, that the coefficients of ΔP_{di} were increased relative to control. The values of *b* and *d* that are required for the predictions of *Eqs. 1* and *2* to match the rib displacements measured with abdominal support are *b* = 0.81 and *d* = 0.56. In other words, the cranial and outward rib displacements produced by a unit rise in ΔP_{di} would be ~20% larger with abdominal support than during control.

The decrease in ΔP_{pl} with abdominal support implies that the descent of the diaphragm was smaller and, thus, that the zone of apposition was larger throughout inspiration. This finding, in agreement with the increase in the rib displacements produced by a unit rise in ΔP_{di} , is fully consistent with the

conventional wisdom that abdominal support causes an increase in the appositional component of diaphragm force. However, the smaller descent of the dome of the diaphragm also implies that the muscle fibers during inspiration were longer, and indeed ΔP_{di} with abdominal support was greater while neural inspiratory drive was unchanged. As a result, the muscle fibers exerted not only a greater appositional force but also a greater insertional force on the lower ribs. In addition, as during control breathing, the rib 10 trajectories during breathing with the abdominal support took place between the trajectories produced by external forces in the craniodorsal and lateral directions (Fig. 3), thus confirming that the force exerted on the lower ribs by the diaphragm in this condition still had both an appositional component and an insertional component. The rib trajectories with abdominal support, in fact, were essentially the same as those observed during control, and the vector analysis yielded the result that on average, the insertional and appositional components contributed nearly equally to the larger rib displacement. On the basis of these considerations, the conclusion may therefore be drawn that abdominal support enhanced both the appositional component and the insertional component of diaphragm force.

Although, as discussed above, the primary cause of the increase in the insertional component lies in the force-length relationship of the diaphragm muscle fibers, abdominal support might also alter the direction of the muscle fibers along part of the line of insertion. In supine dogs, the zone of apposition in the ventral region of the rib cage is very small at FRC (2), as it is in humans (18). Also coordinated contraction of the diaphragm and inspiratory intercostals in intact dogs causes the muscle fibers of the costal diaphragm to shorten by 15–17% of their resting FRC length (L_r) (19), and it is reasonable to assume that in our animals breathing with the diaphragm alone, diaphragm shortening in the control condition was even greater. In the control condition, therefore, the zone of apposition in the ventral rib cage was likely eliminated during the course of inspiration. However, it would be expected that with abdominal support, the zone of apposition in this region would increase, so that the diaphragm muscle fibers would maintain a cranial orientation throughout inspiration. Such a change in orientation might add to the appositional component to produce a larger rib displacement for a unit ΔP_{di} .

The procedure used to support the abdomen in the present study differs from that in quadriplegic subjects. Because the comparison of the rib trajectories (Fig. 3) required that the end-expiratory position of the ribs be unaltered and their displacement during breathing be unimpeded, support in the animals was provided by applying a plate on the ventral abdominal wall at end-expiration. On the other hand, support in quadriplegic subjects is provided by wrapping an elastic binder or a pressure cuff tightly around the abdomen. In these subjects, therefore, Pab at end-expiration is increased, lung volume (FRC) is reduced, and the zone of apposition is expanded. It is possible that in this condition, the contribution of the appositional component of diaphragm force to the lower rib cage expansion is greater than that of the insertional component. The expansion of the zone of apposition at end-expiration in quadriplegic subjects, however, implies that the diaphragm muscle fibers are lengthened, so the insertional component must also be increased.

Mechanism of the decreased expiratory displacement of the upper rib cage. Previous studies in rabbits and dogs have shown that the inward and caudal displacement of the upper ribs during isolated phrenic nerve stimulation is abolished when stimulation is performed in the presence of pneumothorax (3). As a result, the view has long been held that the action of the diaphragm on the upper ribs is exclusively determined by the fall in Ppl. In our animals, however, whereas ΔP_{pl} in the presence of abdominal support was 90% of the value recorded in the control condition, the inspiratory caudal displacement of rib 5 was only 36% of the control value. Thus the decrease in the magnitude of rib 5 displacement with abdominal support was greater than anticipated on the basis of the loss in ΔP_{pl} alone, and this is fully consistent with our hypothesis that this decrease is determined, in part, by the larger cranial displacement of the lower ribs.

With abdominal support, the cranial displacement of rib 10 increased by 1.82 mm, and our previous observations have shown that during the application of external forces to this rib, the cranial displacement of rib 5 was 25% of the cranial displacement of rib 10 (6). Therefore, the increased cranial displacement of rib 10 with the abdominal support should reduce the caudal displacement of rib 5 by (1.82×0.25) mm, or 0.46 mm. In addition, in view of the 10% decrease in ΔP_{pl} , it would be expected that with abdominal support, the caudal displacement of rib 5 would decrease from -1.00 to -0.90 mm. On the basis of these two mechanisms, the predicted caudal displacement of rib 5 would be $-0.90 + 0.46$ mm, or -0.44 mm. This value is reasonably close to the measured displacement (-0.37 mm).

In conclusion, the present studies have shown, in agreement with the conventional wisdom, that the facilitatory effect of abdominal support on the rib cage expanding action of the diaphragm is partly determined by an increase in the appositional force of the diaphragm. The present findings, however, have also shown that 1) about half of the increase in the inspiratory displacement of the lower ribs observed in this condition is determined by the increase in the muscle insertional force and 2) the decrease in the inspiratory caudal displacement of the upper ribs is the result of both the increase in the cranial displacement of the lower ribs and the decrease in ΔP_{pl} .

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: A.D.T. conception and design of research; A.D.T. performed experiments; A.D.T. analyzed data; A.D.T. and T.A.W. interpreted results of experiments; A.D.T. prepared figures; A.D.T. drafted manuscript; A.D.T. and T.A.W. edited and revised manuscript; A.D.T. and T.A.W. approved final version of manuscript.

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