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On the respiratory function of the ribs

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Capello, Matteo, and André De Troyer. On the respiratory function of the ribs. *J Appl Physiol* 92: 1642–1646, 2002; 10.1152/jappphysiol.01053.2001.—To assess the respiratory function of the ribs, we measured the changes in airway opening pressure (Pao) induced by stimulation of the parasternal and external intercostal muscles in anesthetized dogs, first before and then after the bony ribs were removed from both sides of the chest. Stimulating either set of muscles with the rib cage intact elicited a fall in Pao in all animals. After removal of the ribs, however, the fall in Pao produced by the parasternal intercostals was reduced by 60% and the fall produced by the external intercostals was eliminated. The normal outward curvature of the rib cage was also abolished in this condition, and when the curvature was restored by a small inflation, external intercostal stimulation consistently elicited a rise rather than a fall in Pao. These findings thus confirm that the ribs play a critical role in the act of breathing by converting intercostal muscle shortening into lung volume expansion. In addition, they carry the compression that is required to balance the pressure difference across the chest wall.

mechanics of breathing; rib cage mechanics; intercostal muscles

RIBS ARE A PROMINENT FEATURE of the trunk in vertebrates and are often regarded as a shield protecting the vital organs of the thoracic cavity, in particular the heart and the lungs. In mammals, however, many ribs are exposed to pleural pressure, which is below atmospheric pressure. Moreover, ribs move cranially during the inspiratory phase of the breathing cycle. This cranial movement is primarily related to the contraction of two sets of intercostal muscles, namely the internal intercostals of the parasternal area (the so-called parasternal intercostals) (2, 3, 7, 9) and the external intercostals of the rostral interspaces (1, 7, 11), and contributes significantly to the expansion of the lung. Thus, in addition to protecting the intrathoracic organs, the ribs would appear to provide two essential respiratory functions. First, they would constitute the structural elements that carry the compressive stresses that balance the pressure difference across the chest wall. Second, the ribs would transform intercostal muscle shortening into lung volume expansion. Two series of experiments were designed to test these hypotheses, and they form the basis of the present report.

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METHODS

The studies were carried out on 14 adult mongrel dogs (body wt = 13–28 kg) and were approved by the Animal Ethics and Welfare Committee of the Brussels School of Medicine. Animals were anesthetized with pentobarbital sodium (initial dose = 30 mg/kg iv), placed in the supine posture, and intubated with a cuffed endotracheal tube. They were then connected to a mechanical ventilator (Harvard pump, Chicago, IL), and a venous cannula was inserted in the forelimb to give maintenance doses of anesthetic (3–5 mg/kg); a catheter was also inserted into the left femoral artery to monitor blood pressure and heart rate. The rib cage and intercostal muscles were subsequently exposed from the first to the tenth rib by deflection of the skin and underlying muscle layers, and a pair of linearized magnetometers (Norman H. Peterson, Boston, MA) was attached to the external intercostal muscles in the fifth and sixth interspaces on the right and left sides to measure changes in rib cage transverse diameter (12). A differential pressure transducer (Validyne, Northridge, CA) was also connected to a side port of the endotracheal tube to measure airway opening pressure (Pao), after which two experimental protocols were followed.

Experiment 1. Seven animals were first studied to assess the role of the ribs in the inspiratory action of the parasternal intercostals. In each animal, the muscles in two interspaces between the third and the sixth were thus prepared for electrical stimulation on both sides of the sternum by using the procedure previously described (4, 5). Briefly, the most ventral portion of the external intercostal muscle was severed in each interspace, and the caudal border of the rostral rib was cleared of periosteum over the 2–3 cm lateral to the costochondral junction. A curved, chisel-edged instrument was then passed under the rib to separate the periosteum from the bone, and the periosteum was incised so as to expose the internal intercostal nerve. The freed sector of the nerve was then laid over a bipolar stimulating electrode, and a pair of stainless steel hook electrodes, spaced 3–4 mm apart, was implanted into the parasternal intercostal muscle, 1 cm lateral to the sternum, to determine the voltage for supramaximal nerve stimulation. Electromyogram signals thus obtained were amplified (model 830/1, CWE, Ardmore, PA), band-pass filtered below 5 and above 2,000 Hz, and rectified before their passage through leaky integrators with a time constant of 0.2 s. Each nerve thus selected for investigation was subsequently sectioned ~2 cm dorsal to the site of stimulation so as to prevent antidromic stimulation of the internal interosseous intercostal muscles. Sectioning the nerves also avoided stimulation of the spindle afferent fibers, which are known to have extrasegmental projections (8) and

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could have produced contraction of intercostal muscles in adjacent interspaces.

After this procedure was completed, the animal was made apneic by mechanical hyperventilation, the endotracheal tube was occluded at resting end expiration [functional residual capacity (FRC)], and square pulses of a 0.2-ms duration and supramaximal voltage were applied at a frequency of 20 impulses/s to the four internal intercostal nerves simultaneously. At least three trials of stimulation were performed in each animal. The nerves were then covered with warm mineral oil, after which ribs 3–8 were removed on both sides of the chest. In preliminary experiments, attempts were made to remove the entire costal arches. These attempts, however, indicated that the costal cartilages could not be removed without causing major damage to the parasternal intercostals. For each rib, therefore, the periosteum was incised from the costochondral junction ventrally to the angle of the rib dorsally, and by using the chisel-edged instrument already used to expose the internal intercostals nerves, it was carefully slit and peeled on both the external and the internal aspect of the rib. The bony ribs thus exposed were subsequently sectioned at their ventral and dorsal ends. As a result, although the costal cartilages were maintained, a large fraction of the right and left lateral walls of the cage was made of bands of periosteum connected by intact intercostal muscles with intact intercostal nerves and vessels (Fig. 1). No damage was made to the pleura in any animal. Tetanic, supramaximal stimulation of the four internal intercostal nerves was repeated in triplicate.

Experiment 2. Seven animals were next studied to examine the role of the ribs in the action of the external intercostal muscles in the rostral interspaces. The experimental procedure and recording techniques were essentially the same as in *experiment 1*, but the muscles were stimulated by using the technique described by Ninane et al. (13). After rib cage exposure, pairs of copper threads 0.5 mm in diameter were thus inserted bilaterally between the external and internal intercostal muscles in the third and fourth or the fourth and fifth interspaces. In each interspace, the threads were introduced near the costochondral junctions and driven dorsally, parallel to each other, along the cranial and caudal boundaries until their tip lay in the vicinity of the rib angles. The

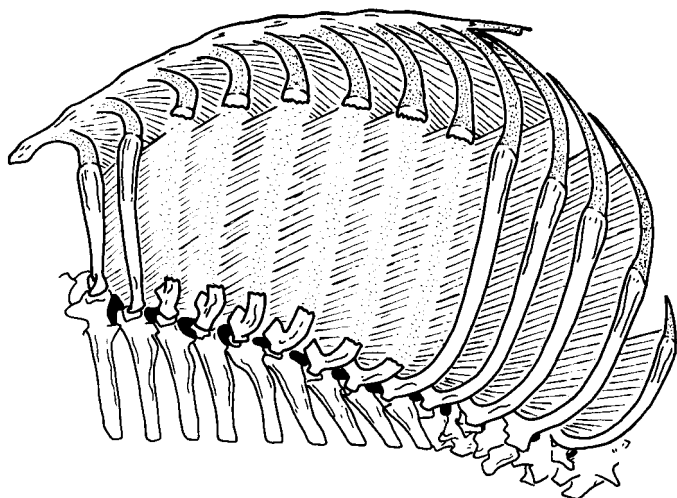


Fig. 1. Diagram of the rib cage after removal of the bony ribs. After ribs 3–8 were removed on both sides of the chest, a large fraction of the lateral walls of the cage was made of bands of external and internal intercostal muscles connected by bands of periosteum.

ventral end of the threads was then bent forward and connected to the stimulator, after which the animal was given an intravenous injection of 2 mg pancuronium. Using square pulses of 60 V and 1-ms duration delivered at a frequency of 50 impulses/s, we could induce selective, clear-cut contraction of the external and internal interosseous intercostals in two contiguous interspaces on both sides of the sternum and elicit a fall in Pao (11, 13). Indeed, in the dog, the external intercostals in the rostral interspaces have both a greater mechanical advantage and a greater muscle mass than the internal intercostals (6). Consequently, when both muscles are simultaneously activated at FRC, the effect of the externals on Pao is predominant. As in *experiment 1*, three trials were obtained in each animal, first with the rib cage intact and then after removal of ribs 3–8.

No changes in blood pressure or heart rate occurred during the course of these experiments; in addition, the pupils in each animal remained constricted and unresponsive to light throughout, thus indicating a deep level of anesthesia. After completion of the measurements, animals were given an overdose (50 mg/kg) of anesthetic.

Data analysis. For each animal, the changes in Pao and rib cage transverse diameter recorded during stimulation with the rib cage intact and after removal of the ribs were averaged over the three trials. Data were then averaged for the animal group, and they are presented as means \pm SE. Statistical comparisons between the changes obtained in the two conditions were made by using paired *t*-tests. The criterion for statistical significance was taken as $P < 0.05$.

RESULTS

Role of the ribs in the action of the parasternal intercostals (experiment 1). Removing the bony ribs induced a substantial alteration in the shape of the rib cage in every animal. Specifically, the normal outward curvature of the lateral walls of the cage was abolished and its transverse diameter at FRC was markedly reduced. For the seven animals, the diameter with the rib cage intact averaged 102.9 ± 5.0 mm, whereas, after removal of the ribs, the diameter was only 77.2 ± 3.6 mm ($P < 0.001$).

Removing the bony ribs also had a major effect on the changes in Pao and rib cage transverse diameter produced by the parasternal intercostals. A representative example of the traces obtained during stimulation of the muscles with the rib cage intact and after removal of the ribs is shown in Fig. 2A, and the changes in Pao recorded in the individual animals are shown in Fig. 2B. Stimulation with the rib cage intact caused a fall in Pao and an increase in rib cage transverse diameter in all animals, thus confirming the inspiratory action of the muscles (3, 5). The change in Pao obtained in the seven animals averaged -3.86 ± 0.25 cmH₂O, and the increase in rib cage diameter was 4.7 ± 0.9 mm. However, when stimulation was performed after removal of the ribs, the change in Pao was reduced to only -1.25 ± 0.08 cmH₂O ($P < 0.001$) and the increase in rib cage diameter was consistently reversed into a decrease (4.0 ± 0.5 mm; $P < 0.001$). Electromyogram activity recorded from the parasternal intercostals after rib removal, however, amounted to $98.3 \pm 4.5\%$ of the activity recorded with the rib cage

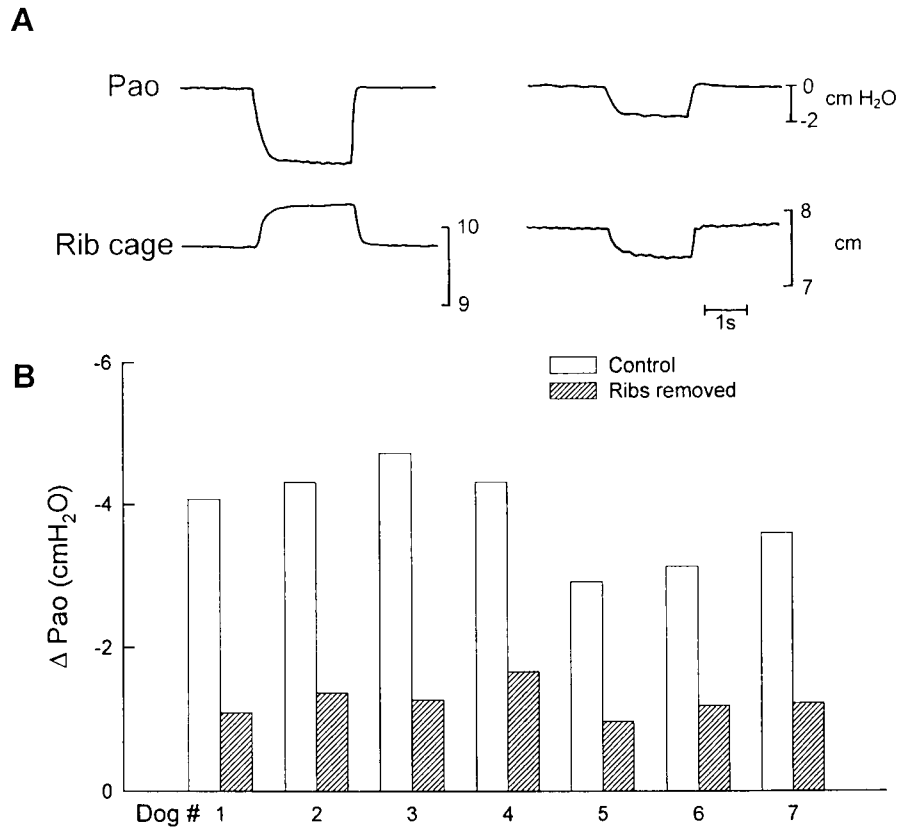


Fig. 2. Effect of rib removal on the action of the parasternal intercostals. *A*: traces of airway opening pressure (Pao) and rib cage transverse diameter obtained during stimulation of the parasternal intercostals in the fourth and sixth interspaces in a representative animal before (*left*) and after (*right*) removal of ribs 3-8. *B*: changes in Pao (Δ Pao) recorded in the 7 animals. Note that the fall in Pao in all animals was smaller after removal of the ribs. Note also that the rib cage diameter at resting end expiration was markedly reduced and that the increase in diameter during stimulation was reversed into a decrease.

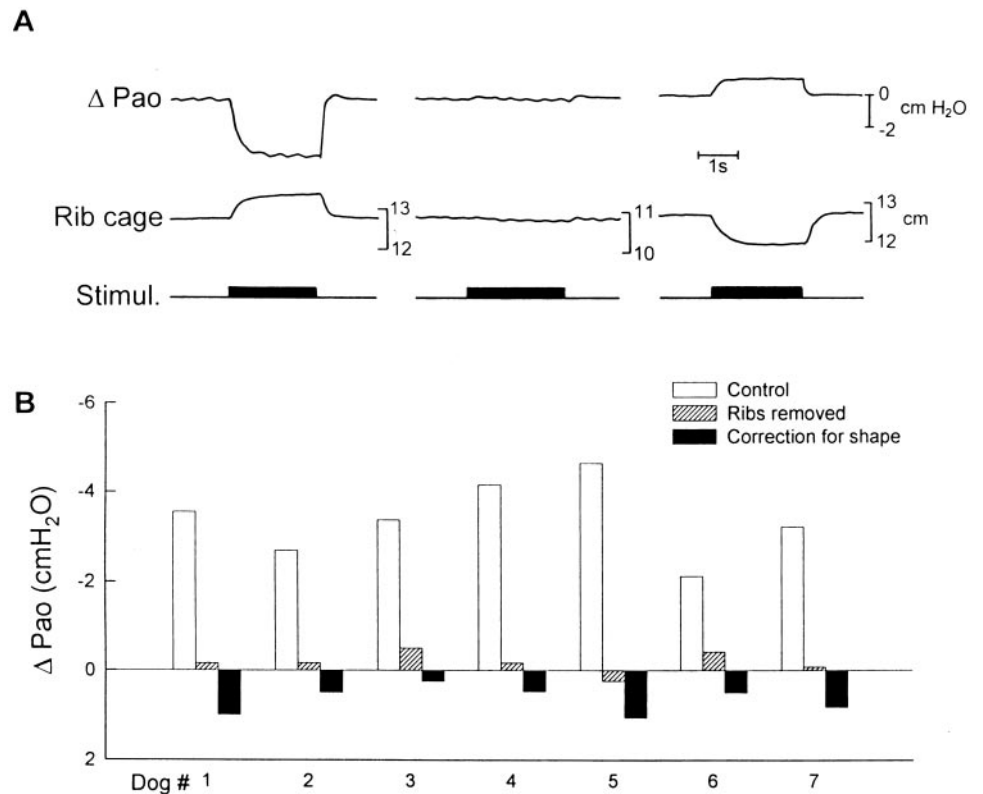


Fig. 3. Effect of rib removal on the action of the interosseous intercostals. *A*: traces of Pao and rib cage transverse diameter obtained during stimulation (stimul) of the interosseous intercostals in the fourth and fifth interspaces in a representative animal with the rib cage intact (*left*), after removal of ribs 3-8 (*middle*), and after the rib cage transverse diameter at end expiration was restored to its control value by a small inflation (*right*). *B*: changes in Pao recorded in the 7 animals. Note that the fall in Pao and the increase in rib cage diameter were eliminated after removal of the ribs. However, when the rib cage diameter at end expiration was restored to its control value, stimulation resulted in a decrease in rib cage diameter and a rise in Pao.

intact, thus confirming that the motor supply to the muscles was well preserved.

Role of the ribs in the action of the external intercostals (experiment 2). Figure 3A shows the records of the changes in Pao and rib cage transverse diameter produced by the external and internal intercostal muscles in two adjacent interspaces before and after removal of the ribs in a representative animal. In agreement with the previous observations of Ninane et al. (13) and Legrand and De Troyer (11), stimulating the interosseous intercostal muscles in two rostral interspaces with the rib cage intact invariably resulted in a fall in Pao and an increase in rib cage transverse diameter. These changes in Pao and diameter were thus similar to those produced by the parasternal intercostals (*experiment 1*) and averaged -3.40 ± 0.32 cmH₂O and 5.7 ± 0.8 mm, respectively. However, when the ribs were removed, the fall in Pao and the increase in rib cage diameter were essentially eliminated (Fig. 3, A and B). For the seven animals, the change in Pao in this condition was only -0.18 ± 0.09 cmH₂O ($P < 0.001$) and the change in rib cage diameter was a small (1.0 ± 0.7 mm) decrease ($P < 0.001$).

As in *experiment 1*, removing the ribs also elicited a disappearance of the outward curvature of the lateral walls of the rib cage at FRC and caused a reduction in the rib cage transverse diameter from 121.4 ± 5.6 to 100.6 ± 6.7 mm ($P < 0.001$). This alteration in rib cage shape might have adversely affected the inspiratory action of the external intercostal muscles independent of the absence of the bony ribs. To evaluate the influence of this confounding factor, we inflated the respiratory system with 300–500 ml until the rib cage transverse diameter in each individual animal was precisely restored to its control value (i.e., until the rib cage had regained its normal outward curvature), and we performed three additional trials of stimulation. As shown in Fig. 3, these stimulations caused a small but definite rise in Pao in all animals ($+0.66 \pm 0.11$ cmH₂O) and induced a clear-cut decrease in the rib cage transverse diameter (4.9 ± 0.8 mm).

DISCUSSION

The current studies have provided the first direct experimental evidence that the ribs have important respiratory functions. When the bony ribs in our animals were removed, the lateral walls of the rib cage collapsed and its normal outward curvature was suppressed. The end-expiratory volume of the cage was thus diminished, and it is likely that the end-expiratory volume of the lung was diminished as well. Also, the fall in Pao produced by the parasternal intercostals was reduced by about two-thirds (Fig. 2), and the fall produced by the external intercostals was abolished (Fig. 3). When the outward curvature of the cage was restored by a small inflation, the external intercostals even induced a decrease in rib cage diameter and a rise in Pao; that is, the normal inspiratory action of these muscles was reversed into an expiratory action. These alterations establish that the ribs do indeed carry com-

pressive stresses and play a critical role in allowing the parasternal and external intercostals to inflate the lung.

The finding that the loss of inspiratory effect after removal of the ribs is greater for the external intercostals than for the parasternal intercostals can probably be accounted for on the basis of the different attachments of the two muscles. The parasternal intercostals attach to the sternum and the costal cartilages. Both structures were maintained in our animals. Consequently, after the bony ribs were removed, the muscles continued to pull the cartilages cranially. To the extent that the costal cartilages of ribs 3–8 in the dog represent ~30–40% of the total length of the ribs, this displacement alone would be expected to induce a

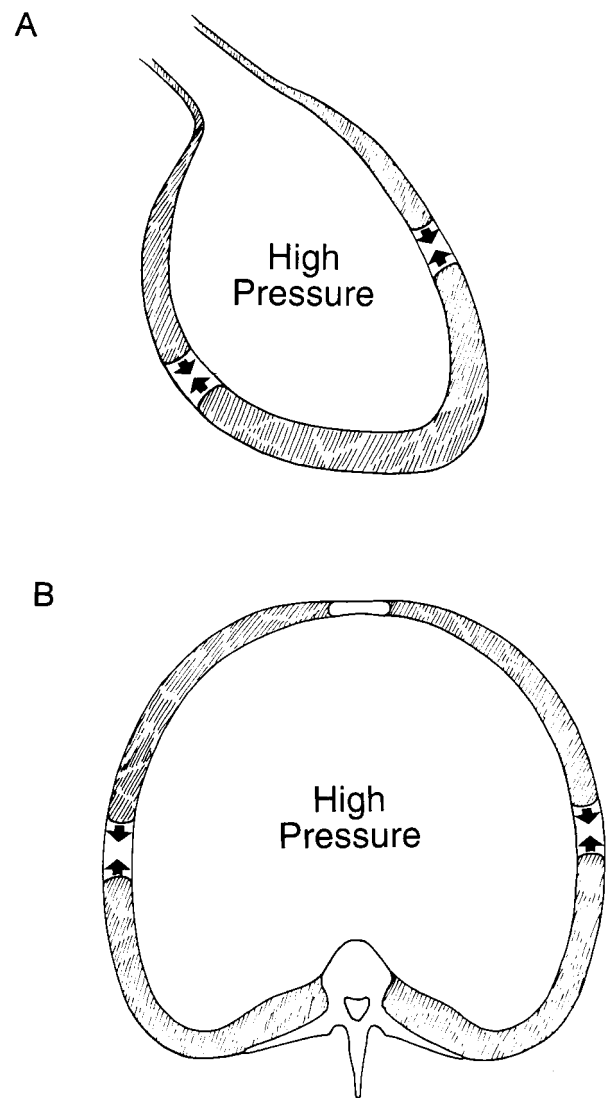


Fig. 4. Mechanism of the expiratory action of the interosseous intercostals after removal of the ribs. A: ventricular myocardium. Contraction of the muscle fibers (arrows) causes intraventricular pressure to rise. B: interosseous intercostals after removal of the bony ribs [the normal (outward) curvature of the rib cage has been restored by inflation]. Contraction of the muscle fibers (arrows) leads to a rise in intrathoracic pressure.

small fall in intrathoracic pressure and cause a (passive) decrease in rib cage transverse diameter. On the other hand, the external intercostals attach only to the bony ribs. Therefore, after these were removed, the muscles formed a series of muscular bands surrounding the thoracic cavity in much the same way as the muscle fibers of the ventricular myocardium encircle the ventricular chamber (Fig. 4). When the ventricular fibers develop tension during systole, they cause intraventricular pressure to rise. Similarly, when unsupported bands of intercostal muscles were made to develop tension, they induced a compression of the thoracic walls, leading to a rise in intrathoracic pressure.

These considerations highlight fundamental differences between the mechanics of the respiratory pump and the mechanics of the cardiac pump. For the heart, the pressure inside the chamber is higher than the surrounding pressure, and the wall must carry tension to balance this pressure difference. Moreover, during contraction, work in the wall is done by reducing the volume of the chamber. Both of these requirements are fulfilled by the properties of muscle. That is, muscles carry tension and perform work as they shorten. In contrast, for the respiratory pump, the pressure inside the wall is lower than the surrounding pressure, and work is done by increasing the volume enclosed by the wall. The properties of muscle do not match these requirements. One solution to this problem is to reverse the curvature of the wall. This is the case for the diaphragm. As it is concave outward, it may carry tension to balance the pressure difference across the wall and induce an increase in the enclosed volume when it shortens. However, the rib cage is concave inward, so it requires elements that carry compression and that convert muscle shortening into volume expansion. As shown in the studies here reported, the ribs are these structural elements.

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