Respiratory function of the rib cage muscles

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ABSTRACT: Elevation of the ribs and expansion of the rib cage result from the co-ordinated action of the rib cage muscles. We wished to review the action and interaction of the rib cage muscles during ventilation.

The parasternal intercostal muscles appear to play a predominant role during quiet breathing, both in humans and in anaesthetized dogs. In humans, the parasternal intercostals act in concert with the scalene muscles to expand the upper rib cage, and/or to prevent it from being drawn inward by the action of the diaphragm. The external intercostal muscles are considered to be active mainly during inspiration, and the internal intercostal muscles during expiration.

The respiratory activity of the external intercostals is minimal during quiet breathing both in man and in dogs, but increases with increasing ventilation. Inspiratory activity in the external intercostals can be enhanced in anaesthetized animals and humans by inspiratory mechanical loading and by CO₂ stimulation, suggesting that the external intercostals may constitute a reserve system, that may be recruited when the desired expansion of the rib cage is increased. The triangularis sterni is an important expiratory muscle during quiet breathing in animals, but it is not active during quiet breathing in man. However, during expiration below functional residual capacity (FRC), and during speech, laughing and coughing, the triangularis sterni is recruited and plays an increasingly important role.

Rib cage muscles serve a dual function. Firstly, they have postural activities. Neck accessory muscles, such as the sternocleidomastoid and scalene muscles, flex the neck and rotate the head. The internal intercostals of one side and the external intercostals of the other side are activated, in concert, to rotate the trunk, and both layers of intercostals on one side are activated, simultaneously, to flex the trunk laterally [1, 2]. Secondly, the rib cage muscles are distinct from other skeletal muscles because they are important respiratory pump muscles. In this regard, the rib cage muscles and diaphragm have to contract rhythmically, and generate the required force to maintain ventilation throughout life.

The respiratory function of the rib cage muscles, particularly the intercostal muscles, has been a subject of considerable controversy throughout medical history, and until the middle of this century, when the physiological techniques improved, the most varying points of view have been taken by physiologists. Recently, our understanding of the action of each group of rib cage muscles and their interaction has been considerably improved. In a motion as complex as that involved in rhythmic expansion of the rib cage, many rib muscles may be active simultaneously, and contraction of several muscle groups in a co-ordinated way is important in maintaining the mechanical advantage of individual muscles, and in causing expansion of the rib cage without distortion. This article attempts to provide an overview of the action and interaction of the rib cage muscles during ventilation.

Functional anatomy of the rib cage muscles

The scalene muscles

In humans, the scalene muscles consist of three bundles, originating from the transverse processes of the lower five cervical vertebrae, and inserting into the upper surface of the first two ribs. Histochemically, the scalene muscles comprise a higher portion (59%) of slow-twitch fibres (I), whereas the relative occurrence of fast-twitch fibres (II) is 22% for Ia and 17% for Ib [3]. Muscles composed primarily of slow-twitch fibres develop and dissipate tension slowly, whereas the converse is true of muscles composed primarily of fast-twitch fibres. Slow-twitch fibres fatigue less during repetitive contractions than Ib fibres, whereas Ia fibres are able to maintain tension in a similar fashion to slow-twitch fibres.

Recent electromyographic (EMG) studies on the scalene muscles have indicated that they are consistently active in humans during quiet inspiration [4]. Data on upper rib cage motion have indicated that the scalene muscles in humans are important inspiratory muscles, and that...
their contraction during inspiration contributes to upper rib cage expansion [5].

The scalene muscles in dogs are distinct from humans in one major aspect. Anatomically, in the dog, the medial portion of the muscles inserts into the outer surface of the 7th or 8th rib laterally, rather than into the first two ribs. This anatomical insertion suggests that the scalene muscles in the dog expand the middle rib cage, as well as the upper rib cage, when they contract. Indeed, selective stimulation of these muscles in dogs produces important cranial displacement of the 7th rib, and increased the anteroposterior and transverse dimensions of the rib cage [6]. However, anaesthetized dogs, in general, do not contract the scalene muscles during quiet breathing, or after phrenicotomy [7], or acute hyperinflation [8]. Therefore, the inspiratory contraction of the ribs and the expansion of the rib cage in these anaesthetized animals must be the result of rib cage muscle contraction, i.e. contraction of parasternal intercostals, external intercostals, levator costae and/or triangularis sterni. This animal model is ideally suited to study the mechanical contribution of these muscles to rib cage expansion.

**The sternocleidomastoid muscles**

The sternocleidomastoid muscles in humans run between the mastoid process and the ventral aspect of the manubrium sterni and the medial third of the clavicle. Intuitively, during contraction, upper rib cage expansion and cephalad motion of the sternum is expected. This was observed during stimulation in dogs [6], and in patients with high tetraplegia [9]. In these patients, the 11th cranial nerve innervating the sternocleidomastoid muscles is preserved, whilst other neck accessory and rib cage muscles are paralysed. The sternocleidomastoid muscles profoundly hypertrophy in these patients, but can only sustain ventilation for a few hours [10]. In normal subjects, they are not active during quiet breathing, unlike the scalene muscles.

**The triangularis sterni**

The triangularis sterni, also called the transversus thoracis or sternocostalis, is a flat muscle that lies deep to the sternum and the parasternal intercostal muscles (fig. 1). Its fibres originate from the dorsal aspect of the caudal half of the sternum, and run cranially and laterally to insert into the inner surface of the 2nd to the 7th costal cartilages. Its anatomy is similar in humans and dogs, although the intersubject variability of its mass is greater in humans (G. Denerle, personal communication). Its fibre orientation is perpendicular to the fibre orientation of the parasternal intercostals and, thus, the triangularis sterni is ideally suited to oppose the action of the parasternal intercostals [11]. Indeed, when the triangularis sterni acts alone in apnoeic animals, it causes a caudal displacement of the ribs and a cranial displacement of the sternum, resulting in a rise in pleural pressure and a decrease in lung volume [12]. Therefore, it has an expiratory action on the rib cage.

Recent studies in dogs [12], have demonstrated that, during quiet breathing, there is invariably a rhythmic activation of the triangularis sterni in phase with expiration. This phasic expiratory activity in the triangularis sterni is of large amplitude, and causes the ribs to be more caudal and the sternum more cranial during the expiratory pause than during relaxation [12]. These findings strongly suggest that, in contrast to humans, expiration in dogs is not a passive process, and the end-expiratory volume of the rib cage is actively determined and maintained below its relaxation volume by the contraction of the triangularis sterni throughout expiration.

In addition, the use of the triangularis sterni during expiration supports inspiration. By initiating inspiration from a volume lower than relaxation volume, the relaxation of the triangularis sterni at the beginning of inspiration results in rib cage expansion which is passive in nature [13]. Consequently, rib cage expansion during inspiration, virtually, has two sequential components: an initial rapid phase of rib cage expansion due to the relaxation of the triangularis sterni, followed by a second phase of active expansion caused by the contraction of the inspiratory intercostal muscles. Quantitative analysis in anaesthetized dogs has demonstrated that this contribution of the triangularis sterni to rib cage elevation is highly variable, and that approximately 20%, and even up to 50%, of the cephalad displacement of the ribs is passive in the supine position during quiet breathing [13-15]. However, in head-up spontaneously breathing dogs, about two-thirds of the tidal volume results from the relaxation of expiratory muscles; mostly (>80%) due to the action of the abdominal, rather than the rib cage, expiratory muscles [16]. In this way, a significant portion of inspiratory muscle work is taken on by expiratory muscles. The activity of triangularis sterni, thus, reduces to some extent the load on inspiratory muscles.

In humans, the triangularis sterni is not active during quiet expiration. However, during expiration below
functional residual capacity (FRC), during speech, laughing, and coughing, the triangularis sterni is recruited, and may play an increasingly important role [17].

The intercostal muscles

The intercostal muscles are two thin layers of muscular fibres occupying each of the intercostal interspaces: an outer layer, the external intercostals, and an inner layer, the internal intercostals, which have fibre orientations perpendicular to one another [11]. The external intercostals extend from the tubercles of the ribs dorsally to the chondrocostal junction ventrally, and their fibres are orientated obliquely, caudally and ventrally from the rib above to the rib below. In contrast, the internal intercostals extend from the sternocostal junctions to the angles of the ribs dorsally, and their fibres run obliquely, caudally and dorsally from the rib above to the rib below.

However, although the intercostal spaces contain two differently orientated layers of intercostal muscles over the lateral portion of the rib cage, they contain a single layer in their ventral and dorsal portion. Ventrally, between the sternum and the chondrocostal junctions, the only fibres are those of the internal intercostal muscles; they are particularly thick in this region of the rib cage, and they are usually called the parasternal intercostals. Dorsally, from the angles of the ribs to the vertebrae, the muscle fibres are derived from the external intercostals. The latter are duplicated by a triangle-shaped muscle, that runs from the tip of the transverse process of the vertebrae cranially to the angle of the ribs caudally; this muscle is termed the levator costae. The functional anatomy of the intercostal muscles is schematically illustrated in figure 2.

Morphologically, the external and internal intercostal muscles are different. Although they show equal distribution of slow-twitch fibres (I) (62%) [3, 18], the relative occurrence of fast-twitch fibres (II) is different for parasternal and external intercostals, and internal intercostals. The parasternal and external intercostals show an equal distribution of fast-twitch fibres (22% IIa and 19% IIb), whereas the internal intercostals have more IIa fibres (35%), and less IIb fibres (1%) [3, 18]. It has been shown that fibre morphology and contractile properties of the different intercostal muscles are related to their functional difference [18].

The parasternal intercostals are consistently electrically active during inspiration in animals. EMG recordings from intercostal muscles in dogs and cats have demonstrated that the external intercostals, particularly in the cranial portion of the rib cage, and the levator costae are also active in phase with inspiration [19-21]. The phasic inspiratory activation of these muscles is well illustrated by the tracings of an animal shown in figure 3. In contrast, the internal intercostals are only active during expiration, in particular in the caudal part of the rib cage [19].

Fig. 2. — Functional anatomy of the human intercostal muscles, illustrating three sets of intercostal muscles: parasternal, external and internal intercostals. Levator costae is not illustrated.

Fig. 3. — Electromyographic (EMG) activity of parasternal intercostal, external intercostal, and levator costae in the third right interspace in a supine anaesthetized dog, breathing at rest. (From [21], with permission).
Measurements of respiratory changes in muscle length in the dog have indicated that the parasternal intercostals always shorten during inspiration, and lengthen during expiration [22]. Selective denervation of the parasternal intercostal in one interspace virtually eliminates its inspiratory shortening [23]. This is unambiguous evidence that the inspiratory activity of the parasternal intercostals is agonistic in nature, and that the contraction of the parasternal intercostals during inspiration is the cause of rib displacement, rather than the consequence of rib motion. In addition, this observation strongly suggests that the external intercostals and levator costae do not play a major role in causing inspiratory elevation of the ribs during quiet breathing; if they did, then the parasternal intercostals whilst being selectively denervated would continue to passively shorten a certain amount during inspiration [24]. Therefore, it appears that the parasternal intercostals are the primary inspiratory rib cage muscles during quiet breathing, and that the actual contribution of the external intercostals and levator costae to rib cage expansion during quiet breathing is probably limited.

Recent observations in dogs have shown that the inspiratory activity of the external intercostals and levator costae is increased after phrenicotomy [7, 21]. Additional experiments have demonstrated that when the parasternal intercostals are denervated in several interspaces, the levator costae and external intercostals produce rib elevation [14, 21]. Therefore, external intercostals and levator costae have an inspiratory action. When needed, i.e. during inspiratory mechanical loading and CO₂ stimulation [25, 26], they are capable of causing a significant expansion of the rib cage and the lung during breathing.

In humans, the role of the intercostal muscles in respiration is incompletely defined for two reasons. Firstly, it is difficult to deduce their mechanical action on the basis of the geometry of the rib cage; and secondly, there is rather scanty information about the circumstances in which they are electrically active. Recent work has shown that the parasternal intercostals in humans are active during inspiration, with a pattern of activity that resembles that of the diaphragm, and that they can act in concert with the scalene muscles to expand the upper rib cage or to prevent it from being drawn inward by the action of the diaphragm [4, 27, 28]. Less is known about the external intercostals, levator costae and internal intercostals. Taylor [29] found inspiratory activity during quiet breathing in parasternal intercostals and in external intercostals during deep breaths. Recently, increased activity of the external intercostals has been demonstrated in voluntary deep breathing, CO₂ stimulation and mechanical loading [28, 30], suggesting the increasing importance of the external intercostals with increasing ventilation.

Mechanical contribution of rib cage muscles to rib motion

Elevation of the ribs and expansion of the rib cage are the prominent features of the inspiratory phase of the breathing cycle. In contrast to humans, anaesthetized dogs do not contract the scalene muscles during quiet breathing, even after diaphragm paralysis [7]. Thus, the inspiratory elevation of the ribs must be the result of the relaxation of the triangularis sterni and the contraction of the three groups of intercostal muscles, namely, the parasternals, the external intercostals situated in the cranial interspaces, and the levator costae. An attempt has been made to estimate their mechanical contribution to rib elevation in two consecutive series of experiments in supine anaesthetized dogs in our laboratory.

Firstly, we developed a technique for measuring changes in intramuscular pressure in the parasternal intercostal muscles during respiratory manoeuvres, which was demonstrated to be a good index of force developed during parasternal contraction [31]. Secondly, we used the force generated during parasternal contraction, as measured by the changes in intramuscular pressure, to estimate the parasternal contribution to rib elevation. During quiet breathing, the relaxation of the triangularis sterni constitutes the initial passive phase of rib elevation, and shares approximately 50% of the total rib elevation. After subtracting the contribution of the triangularis sterni, about 70% of the rib elevation was due to parasternal contraction, whereas the external intercostals and levator costae shared a lesser role during quiet breathing [15]. Du Toyer [32] recently used parasternal intercostal denervation to quantify the contribution of three groups of inspiratory intercostal muscles to rib elevation, and reached similar conclusions.

However, with diaphragm paralysis, rib cage expansion is markedly augmented in order to maintain adequate ventilation, suggesting the recruitment of rib cage muscles [33]. As the initial rapid phase of rib elevation, caused by the relaxation of the triangularis sterni, is not associated with any appreciable change compared with quiet breathing [34], the augmented rib elevation after diaphragm paralysis must, thus, result from an increment in the second phase of rib elevation. This indicates that the three groups of inspiratory intercostal muscles play a greater role. After diaphragm paralysis, although the parasternals are recruited as well, the relative mechanical contribution of the parasternals decreases, suggesting an increasing importance of the external intercostals and levator costae [15]. Budzinska et al. [35] have recently shown that the external intercostals, when activated maximally by spinal cord stimulation, have the capacity to produce larger falls in tracheal pressure, and larger increases in lung volume, than the parasternals. These observations suggest that the external intercostals constitute a reserve system, that may be called into action when the demand placed on the inspiratory muscles is increased.

It is worthwhile, however, to stress that the work mentioned above pertains to supine anaesthetized dogs. It should not be extended to humans, in which the scalene muscles are known to play an important role, and the triangularis sterni is not active during quiet breathing. Moreover, less is known about the mechanical effectiveness of the external intercostals and levator costae in humans. Their respiratory function needs to be further defined.
Changes in inspiratory mechanical load are known to result in recruitment of the external intercostal muscles. Most importantly, when the airway is blocked during the expiratory pause for a single breath, an increase in external intercostal motor activity occurs, suggesting that this response is mediated by a segmental reflex mechanism, rather than by central respiratory drive [36]. That muscle spindle afferents play a role in its facilitation is further confirmed by the observations that this response is abolished after section of the appropriate thoracic dorsal roots, and persists after vagotomy.

Interaction of rib cage muscles

The ability of the rib cage muscles to expand the rib cage and, consequently, to produce changes in lung volume is determined to a large extent by their co-ordinated action. In a motion as complex as that involved in the expansion of the rib cage, many rib cage muscles are active simultaneously in phase with the breathing cycle. Their interaction or linkage is important in maintaining a mechanical advantage, because the isolated contraction of any one respiratory muscle or one group of respiratory muscles appears to be ineffective. More importantly, their co-ordinated action has been shown to lead to mutual facilitation. In a dog model, more insight has been obtained in rib cage muscle interaction. These data are summarized here.

External intercostal-external intercostal

It is known that the external intercostals in the cranial interspaces and the parasternals are electrically active, and always shorten during quiet breathing and stimulated inspiration. Recent observations in dogs have shown that after denervation in a given interspace, the external intercostal shortening, although significantly less than control values, is still persistent during resting breathing [14], but is markedly reduced following subsequent parasternal denervation in the same interspace [14], or is reversed in lengthening [37]. Parasternal shortening is almost abolished after its denervation during resting breathing [14, 23, 37]. However, after phrenicotomy the parasternal, whilst being denervated, still shortens a significant amount [7]. Thus, the contraction of one intercostal muscle in one interspace causes passive shortening of the other intercostal muscle. These findings indicate that the two muscles in the same interspace are mechanically arranged in parallel; indeed, it is likely that during resting breathing, parasternal contraction contributes, to some extent, to external shortening; however, when the demand placed on the inspiratory rib cage muscles increases, it is likely that the contraction of the external intercostal muscles also contributes to parasternal shortening [14]. These observations suggest that the interaction of these two groups of muscles achieves the desired expansion of the rib cage under different circumstances.

External intercostal-external intercostal

There is, as yet, no direct mechanical evidence on the interaction of the external intercostal muscles in different interspaces. Initial denervation of the external intercostal muscle in a given interspace resulted in an increase in external shortening in the adjacent interspace, without a significant increase in the level of the muscle activity [14]. This suggests that the external intercostal muscles of the lateral rib cage in different interspaces may be arranged in series. As a consequence, rib displacements caused by these muscles are additive and, therefore, maximized.

Parasternal-parasternal

DE TROYER AND FARKAS [7] have shown that, during quiet breathing, parasternal shortening in a given interspace is virtually abolished after its denervation, suggesting that the mechanical interaction of the parasternal intercostals among different parasternals is limited. However, after phrenicotomy the parasternal, whilst being denervated, still shortens a significant amount, suggesting a greater mechanical interaction among interspaces than during quiet breathing.

Alterations in rib cage muscle action with hyperinflation

Several conditions may exert a marked effect on respiratory muscle interaction and may profoundly alter the pattern of rib cage motion. Hyperinflation is an example of such a condition. Hyperinflation is a common functional abnormality accompanying diseases associated with airflow obstruction. Hyperinflation disadvantages the diaphragm [38]. In severe hyperinflation the diaphragm may even have a deflationary effect on the rib cage [8, 39]. In patients with chronic airflow limitation who are severely hyperinflated, a paradoxical motion of the rib cage has been observed during tidal breathing (Hoover's sign). Under these circumstances, the function of the inspiratory intercostal muscles may be much better preserved [39]. We examined the changes in length of the diaphragm and of the parasternal intercostals during hyperinflation in supine anaesthetized dogs, and demonstrated that during acute hyperinflation from FRC to total lung capacity (TLC) the parasternals shortened by 7%, and the diaphragm by more than 30% [39, 40]. As a consequence, hyperinflation is expected to induce a mechanical disadvantage, which is much more pronounced in the diaphragm than in the parasternal intercostals.

Moreover, although the optimal length in the diaphragm is expected to correspond to a lung volume close to FRC [41, 42], the parasternal intercostals were found to approach their optimal length near TLC [43]. This was further confirmed by experiments in which the relationship between electrical input and force output, as estimated by changes in parasternal intramuscular pressure,
was shown to improve with hyperinflation [44]. Therefore, at high lung volume, the parasternal intercostals are better suited for force generation than the diaphragm. It should be emphasized, however, that this was only demonstrated in dogs in the supine position, and that it has not been examined in awake standing dogs. Moreover, acute hyperinflation is distinct from chronic hyperinflation, in that adaptive changes to chronic shortening may occur in the diaphragm [45-48], and, as a consequence, a less severe mechanical disadvantage for the inspiratory muscles is expected.

However, our understanding of how respiratory muscle function is altered in patients with hyperinflation remains limited. Little direct information is available. Indirect evidence suggests that intercostal muscle length changes with hyperinflation are considerably smaller than diaphragmatic length changes [49]. In normal subjects, hyperinflation changes breathing pattern, such that inspiratory rib cage displacement is associated with abdominal indrawing [50]. A similar breathing pattern was observed in patients with severe hyperinflation [51]. Further insight into the action and interaction of rib cage muscles is needed to reach an integrated view on how the action of the vital pump is altered by hyperinflation.

Conclusion

Elevation of the ribs and expansion of the rib cage result from the co-ordinated action of rib cage muscles. Among these, the parasternal intercostals appear to play a predominant role during quiet breathing, both in humans and in anaesthetized dogs, whereas the contribution of the external intercostals seems to be limited. The external intercostals may constitute a reserve system, that may be called into action when the desired expansion of the rib cage is increased. Their function still needs further definition, particularly in humans.

References