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JACOPO P. MORTOLA, GIUSEPPE SANT'AMBROGIO

Mechanics of the trachea

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Fisiologia. — *Mechanics of the trachea* (*). Nota di JACOPO P. MORTOLA e GIUSEPPE SANT'AMBROGIO (**), presentata (***) dal Socio R. MARGARIA.

RIASSUNTO. — Abbiamo studiato le caratteristiche meccaniche della trachea di cane considerando separatamente le sue due componenti: gli anelli cartilaginei e la parete posteriore fibromuscolare. Gli anelli cartilaginei costituiscono essenzialmente il supporto per la parete posteriore che, d'altra parte, muovendosi in dentro ed in fuori come un pistone, contribuisce la maggior parte delle variazioni del volume tracheale. Il volume contribuito dalla componente cartilaginea è quasi interamente nella porzione negativa della funzione pressione-volume. L'accoppiamento meccanico fra anelli cartilaginei e parete posteriore permette ai propriocettori tracheali, localizzati unicamente nella parete posteriore, non solo di segnalare sia la pressione positiva che la negativa ma anche di differenziare fra esse.

While the pressure-volume relationship of the trachea has been studied by many authors, either in vivo or in vitro (Martin and Proctor, 1958; Croteau and Cook, 1961; Olsen, Stevens and McIlroy, 1967; Coburn and Palombini, 1972; Bartlett, Sant'Ambrogio and Wise, 1976), nothing is known about the mechanics of the two parts into which the trachea can be divided, the back wall and the cartilaginous rings. In fact in dogs, cats, rabbits, men and other mammals the cartilage is a "U" shaped structure completed on the posterior part by a fibromuscular component (Vanpeperstraete, 1973).

Mechanically, the cartilaginous rings seem to provide the support to the back wall, which, on the other hand, expanding and collapsing seems to contribute most of the change in tracheal volume.

The mechanical coupling of the back wall and the cartilages could also help to explain the behavior of the airways receptors (Bartlett *et al.*, 1976) of which the slowly adapting stretch receptors have been found to be uniquely located in the smooth muscle of the back wall (Bartlett, Jeffery, Sant'Ambrogio and Wise, 1976) and the rapidly adapting "irritant" receptors all around the tracheal circumference (Sant'Ambrogio, Remmers, de Groot and Callas, 1977).

METHODS

We measured the volume contributed by the cartilaginous rings and the back wall at different tracheal pressures with the same theoretical approach that Konno and Mead (1967) used to define the volume contri-

(*) Department of Physiology and Biophysics and Anesthesiology, University of Texas Medical Branch, Galveston, Texas 77550, USA - Study supported by NIH grant 1 RO 1 HL 20122-01.

(**) Corrispondenza al Dr. J. P. Mortola, Department of Physiology and Biophysics, University of Texas Medical Branch, Galveston, Texas 77550, USA.

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butions of the rib cage and the abdomen-diaphragm within the chest wall. We assumed that both mechanical components of the trachea could be considered "parts", i.e. changing the volume of the trachea each one of them would move as a whole, without motion independence within itself. Then, at different tracheal volumes, any reduction of one of the two parts should determine an expansion of the other, or, according to Konno and Mead's terminology (1967), at each volume the trachea should have only one degree of freedom.

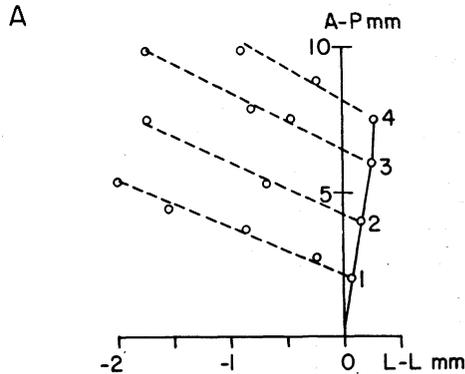
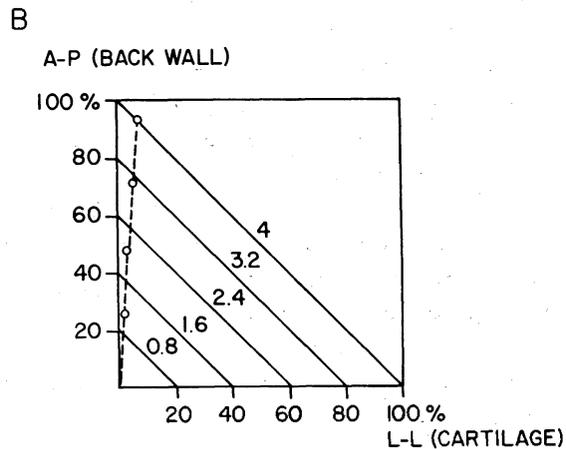


Fig. 1. *A*) A-P (Back wall). L-L (Cartilage) relationship at different tracheal volumes (1-2-3-4 ml) and after restraining isovolumetrically the cartilaginous rings. At different volumes the restraining of the cartilage determines a corresponding expansion of the back wall. The isovolume lines constructed in this way are almost parallel and equidistant for equal volume increments. *B*) the volume contribution of each of the two components (back wall and cartilage) is shown as percent of the maximal volume considered (4 ml) by the dashed line, as derived from panel A. Each of the parallel lines represents the relationship between cartilaginous rings and back wall at different tracheal volume (0.8, 1.6, 2.4, 3.2, 4 ml). If the cartilaginous rings are restrained at their 0 volume, then the volume of the structure is entirely contributed by the back wall.



To prove whether our assumption was correct we plotted at different tracheal volumes the tracheal anterior-posterior (A-P) diameter corresponding to the back wall against the lateral-lateral (L-L) diameter, corresponding to the cartilaginous rings. At different volumes we reduced either the L-L or the A-P diameter, and, provided that the transmural pressure does not increase very much so as to determine some deformation within each of the two parts, the relationship between the two diameters are described by a family of parallel isovolume lines, approximately equidistant for equal volume increments (fig. 1 A). These results show that the trachea can be considered with good approximation a system with only two parts closely interdependent

at different tracheal volumes. On this basis, from the P-V curve of the trachea, for each volume we could calculate the volumes contributed separately by either the cartilaginous rings or the back wall (fig. 1 B), and therefore the P-V relationship for each of the two parts.

The P-V curve of each one of the two components could also be constructed keeping the other part fixed at its position at the lowest tracheal volume considered, i.e. at -35 mm Hg transmural pressure. In fact, in this condition, the increase in volume is only contributed by the part free to expand, and therefore the resulting P-V curve will be the P-V relationship of that component.

Actually, since the two parts are mechanically very different, it is not possible to increase the volume after having fixed the A-P diameter because this leads to a relatively large increase in transmural pressure. Therefore this procedure would introduce a marked deformation (i.e., at each volume the system has more than one degree of freedom) and our assumption is no longer valid.

Therefore it is only possible to keep the L-L diameter fixed at its lowest position (reached at a transmural pressure of ca. -35 mm Hg) so that any increase in volume of the trachea represents the volume contributed only by its back wall. The P-V relationship of the back wall constructed in this way corresponds exactly to that obtained by measuring at each point of the P-V relationship of the trachea the relative volume contributed by the back wall, as described above (fig. 1 B).

Therefore, in order to study separately the volume contributions of the back wall and of the cartilaginous rings, we measured the P-V curve of the trachea, and afterward, having fixed the cartilaginous rings at their lowest position (i.e. at the lowest tracheal volume considered), we repeated the manoeuvre, obtaining the P-V relationship of the back wall. By subtracting this function from that of the whole trachea we could obtain the P-V curve of the cartilaginous rings.

The extrathoracic tracheas of three dogs, weighing 10-12 kg, were used for these studies: the volumes of the tracheal segments averaged 10 ml, and their resting lengths 8 cm. The pressure-volume relationships were obtained by measuring the volume with a calibrated syringe, and the pressure with a Statham pressure transducer. The changes in diameters were measured with isotonic force transducers. The volumes measured at different pressures have been corrected according to Boyle's Law.

RESULTS AND DISCUSSION

Our approach for estimating the separate volume contributions of the cartilaginous rings and of the back wall is based on the comparison between the P-V relationship before and after restraining the cartilages. Considering the many factors involved in determining a P-V relationship, we had to investigate the reproducibility of our results.

Martin and Proctor (1958) observed that when the trachea is either inflated or deflated to a given volume the transmural pressure does not stay constant but shows a progressive change for up to 45 minutes, with 80% of these changes occurring in the first 30 seconds. This pressure decay is a general phenomenon of the elastic structures, and its amount is variable, being related to the physical properties of the tissues (Hill, 1926; Bozler, 1941), the rate of the deformation, the temperature and the "history" preceding the manoeuvre (Remington, 1957, also for references).

When oscillatory inflations and deflations of the tracheal segments are repeated the pressure values show a progressive decrease especially evident during the first cycles. Only after 20-30 cycles do the pressure oscillations appear to have become fairly constant. Coburn and Palombini (1972) have shown that the amount of the pressure decay due to the stress relaxation is linearly related to the active tension of the smooth muscle of the tracheal back wall. Considering the heterogeneity of the tracheal structure, we analyzed separately the stress-strain relationships of each of its two components.

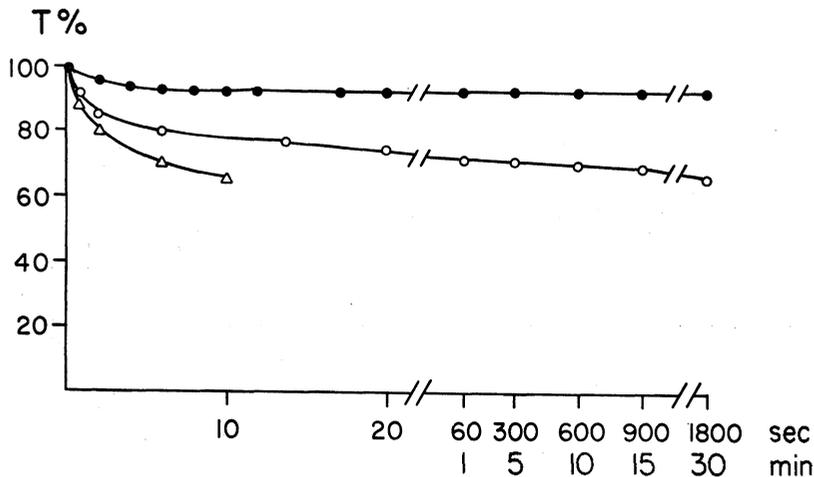


Fig. 2. - Tension decay (in % of the maximal tension) after stretch of the tracheal cartilage (●), of the back wall (○) and of the back wall after removal of its tunica fibrosa (Δ). While the tension of the cartilage after a quick small reduction remains constant, the tension of the back wall decreases during the first 30 minutes, and this decrease in tension appears to become more evident after removal of the tunica fibrosa.

In fig. 2 the tension developed in a fragment of a tracheal cartilage after the application of a maintained stretch decreases during the first seconds (by 8% of the initial value after the first 10 seconds in the example shown in the figure), remaining then practically constant for up to 30 minutes. On the contrary, an analogous tension developed in a stretched back wall of the trachea keeps decreasing throughout the first 30 minutes (by 35% of the initial value in the example shown in the figure), and this decay in tension seems to become even higher after removal of the tunica fibrosa. These findings seem to suggest that all the pressure changes observed during

a maintained inflation or deflation of the trachea are due to the visco-elastic properties of the back wall, and particularly of its smooth muscle.

Considering that after 30 oscillations the P-V curve of the trachea seems to have become almost constant, we applied this many oscillations before any pressure-volume measurements. With this method we have found a very good reproducibility of our results. In any case we have to consider that the trachealis muscle is in tonic contraction during eupnea (Severinghaus and Stupfel, 1955), and that the depth and the frequency of breathing and the smooth muscle tone keep changing (Scarpelli, Real and Rudolph, 1965). Hence we would expect that the mechanics of the trachea "in vivo" might be to some extent different than that resulting from our data.

In fig. 3 are shown the P-V relationships of a tracheal segment as a whole, and separately of its back wall in a dog. In all the experiments, as we would expect from the previous results (fig. 2), the hysteresis observed in the whole trachea is essentially equal to that of the back wall.

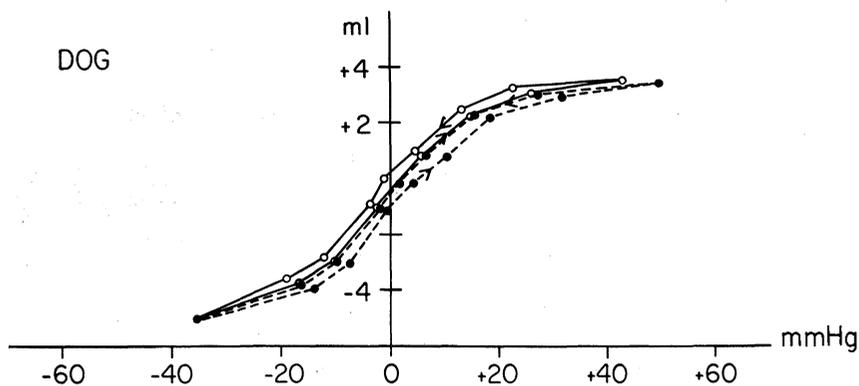


Fig. 3. - Pressure (mm Hg.) Volume (ml) relationship of a dog tracheal segment (continuous line) and of its own back wall (dashed line). The shape and the hysteresis of the two curves are very similar.

The relative volume contribution of the back wall and of the cartilage are shown in fig. 4. The compliance of the trachea appears to be lower with positive than with negative pressures and the general pattern of the P-V curve is similar to that found for this species "in vitro" by other authors (Martin and Proctor, 1958; Olsen *et al.*, 1967).

The back wall appears to contribute most of the changes in volume of the trachea (91%); the cartilage appears to be simply a semirigid support on which the back wall moves outward and inward as a piston. This mechanism allows the receptors located in the back wall to be stretched either with positive or negative transmural pressures.

The cartilage gives its contribution essentially below the resting volume of the trachea. This asymmetry of the cartilage contribution could lead to a lower back wall tension with negative rather than with positive transmural pressures. In fact with negative transmural pressures the radius of curvature

of the back wall, for the closing of the cartilaginous rings, decreases more than with positive pressure, and could even determine a reduction of its tension. This fact could explain the asymmetry of the response of the stretch receptors to maintained positive and negative pressures (Bartlett *et al.*, 1976).

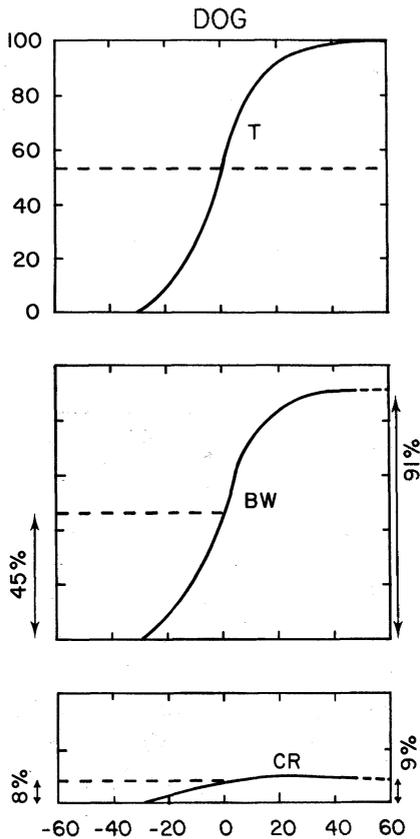


Fig. 4. - Pressure-volume relationship of the back wall (middle panel) and of the cartilaginous rings (bottom panel) of a dog tracheal segment (top panel). One hundred percent volume means the volume displaced by the trachea along the pressure range considered (abscissa). The curves of the whole trachea and of the back wall are the averages of all the experiments considering, at each volume, the mid pressure value between the inflation and deflation curves. The curve for the cartilage is the difference between the first two relationships.

We have also studied the P-V relationship of the trachea after removal of the tunica fibrosa in its posterior wall (fig. 5). The whole structure (thick continuous line) becomes more compliant than in the control condition (thin continuous line), but its hysteresis remains essentially the same. These findings are in agreement with the observation mentioned previously that the decay in tension after stretching the back wall is higher without tunica fibrosa (fig. 2), therefore indicating that within the back wall the tunica fibrosa is stiffer than the smooth muscle, and that the hysteresis of the whole trachea is practically due to the trachealis muscle.

In order to study the applicability of our results "in vitro" to the "in vivo" situation, besides the differences of the visco-elastic properties of the trachea mentioned above, we have to consider two points: the change of the length of the trachea "in vivo", and the influences of other surrounding structures in the neck on its mechanical properties.

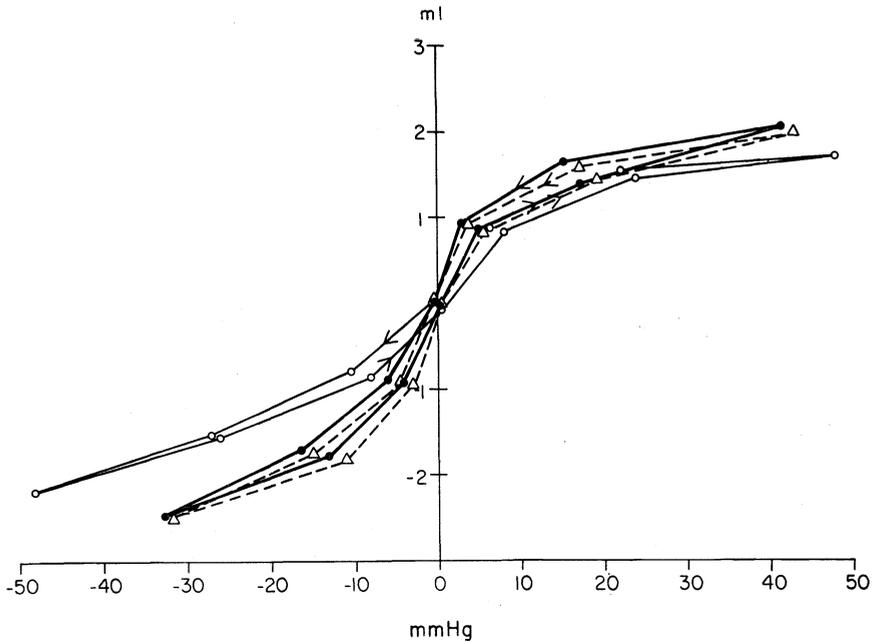


Fig. 5. - Pressure-volume relationships of a dog tracheal segment (thick continuous line) and of its back wall (dashed line) after removal of the tunica fibrosa. The thin continuous line represents the P-V curve of the intact trachea.

Miserocchi and Agostoni (1973) have shown that in the supine dog the trachea is 15.5 % longer than L_0 , where L_0 is the length of the isolated trachea with no acting forces. Hyatt and Flath (1968), in studies on isolated bronchi of dog, found that the pressure-diameter relationships were not different at different lengths. In the trachea of two dogs we have studied the P-V relationship at different lengths above and below L_0 (fig. 6). While the shortening below L_0 makes the trachea less compliant, the lengthening up to 125 % of L_0 changes the shape of the curve very little.

Even if the longitudinal forces acting on the trachea do not seem to markedly affect its P-V relationship, this does not necessarily mean that the structures providing these forces are not affecting per se the partitioning of the tracheal volume. We could speculate that all the tissue connecting the trachea to the vertebral column, either in the neck or in the thorax, could interfere with the motion of its back wall. On the other hand the ventral ligaments, fixing the trachea either directly or indirectly to the rib cage, probably do not interfere with the small motion of the cartilaginous rings. Altogether, we would expect that the structures surrounding the trachea could interfere mainly with the outward motion of the back wall therefore reducing the compliance of the whole trachea with positive pressure and also reducing the relative volumetric contribution of the back wall. In agreement with these considerations the portion of our P-V relationship with negative pres-

tures is very similar to that found in an isolated "in situ" tracheal segment by Bartlett *et al.* (1976), while the portion with positive pressures has a compliance more than double that shown in the trachea "in situ".

In conclusion, the "U" shaped cartilaginous rings are the support of the back wall which moving outward and inward as a piston contribute the changes in volume of the trachea.

This arrangement prevents the collapse of the trachea and at the same time does not interfere with the ventilation as would have been the case with a completely rigid cartilaginous structure (Macklin, 1929). On the other hand the mechanical coupling between back wall and cartilage allows the stretch receptors not only to signal either positive or negative transmural pressures but also to differentiate between them.

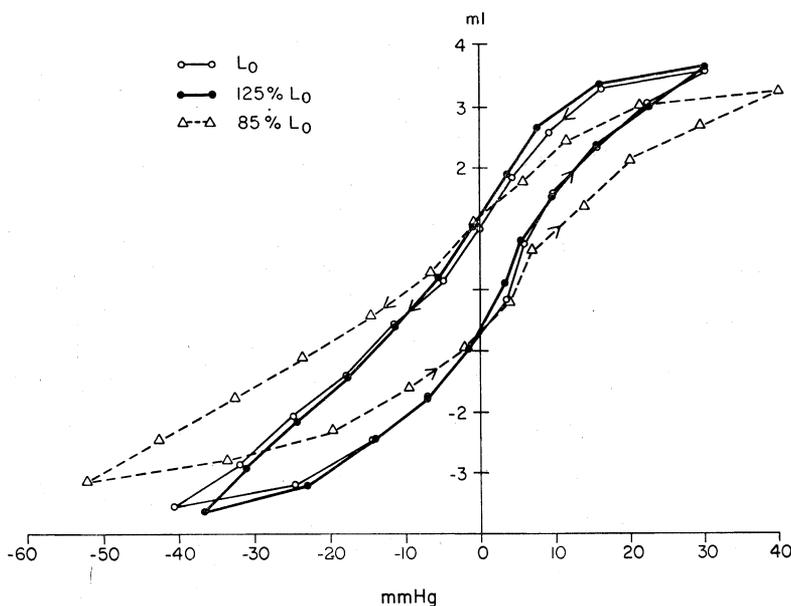


Fig. 6. - Pressure-volume relationships of a dog isolated tracheal segment at zero force (L_0 , ○), after lengthening to 125% of its L_0 (●) and after shortening to 85% of its L_0 (△). While the lengthening does not essentially affect the P-V relationship, after shortening the compliance of the trachea decreases.

The tension behaviors after stretching of the cartilage and of the back wall, and the fact that the airways slowly adapting stretch receptors have been found uniquely located in the smooth muscle of the back wall (Bartlett *et al.*, 1976), while the rapidly adapting receptors have been found all around the airway circumference (Sant'Ambrogio *et al.*, 1977), could suggest that both of the two types of receptors are stimulated by the tension changes and that their different responses might be related to the different mechanical properties of the tissue in which they are embedded.

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