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Stretch receptors of the trachea

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

RIASSUNTO. — I tensorecettori situati nella parete posteriore della trachea sono stati studiati paragonando la loro risposta alla trazione trasversale direttamente applicata alla parete posteriore ed alla pressione transmurale applicata alle vie aeree. Questi recettori segnalano sia la tensione che la sua variazione in funzione del tempo: la loro risposta dinamica dipende dalle proprietà visco-elastiche del muscolo liscio tracheale in cui sono situati. I segnali che originano da questi meccano recettori in risposta a pressioni transmurali sia positive che negative sono interpretati in dipendenza dell'accoppiamento meccanico tra gli anelli cartilaginei incompleti e la parete posteriore membranosa.

Tracheal slowly adapting stretch receptors are uniquely located in the membraneous back wall and, more precisely, in the trachealis muscle and are activated by a transversal stretch of this portion of the airway (Bartlett

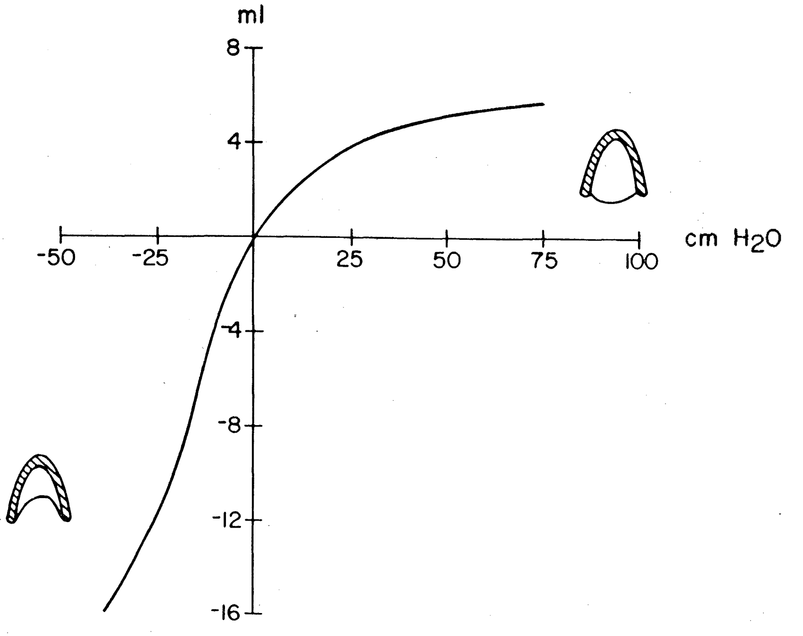

Fig. 1. - Relationship between volume (ml) and transmural pressure (cm H_2O) of a tracheal segment. The two insets show that the membraneous posterior wall is stretched both with positive (outward) and negative (inward) pressures. (Re-drawn from Bartlett *et. al.*, 1976).

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et al., 1976). The mechanical coupling between the cartilagineous rings and the back wall accounts for their response to either positive or negative transmural pressures (fig. 1): the semirigid support provided by the cartilagineous rings to the membraneous posterior wall allows this latter structure to be stretched both with positive (moving outward) and negative (moving inward), pressures. With a homogeneous structure there would be only the possibility of an outward stretching with positive transmural pressure.

In this study we compared the response of tracheal stretch receptors to the more direct stimulation of stretching a fragment of the posterior wall " in situ " and to transmural pressure applied across the intact airways.

METHODS

We used 7 dogs anesthetized with pentobarbital (30 mg/kg i.v.). The trachea was cannulated at the level of the cricoid cartilage; thin filaments dissected out of the peripherical cut end of the right vagus nerve were used to record unit activity originating from slowly adapting stretch receptors. Only receptors located in the extra-thoracic trachea were considered; they were located by directly probing this portion of the trachea through a cuffed catheter. Their response to transmural pressure was established before and after fixation of the cartilage corresponding to the receptor site by means of a clamp. This clamping reduced the lateral dimension of the cartilagineous ring at its position at — 35 cm H_2O. Then the extrathoracic trachea was cut along its anterior aspect and the fragment of the back wall site of the receptor was fixed to a rigid support through the cartilage on one side and to a movable arm attached to the motor on the other side. Either a maintained or a sinusoidal stretch could be applied to the fragment in order to activate the receptor.

RESULTS AND DISCUSSION

Response to transversal stretching.

These slowly adapting stretch receptors are responding only to transversal but not to longitudinal stretching of the back wall. Fig. 2 shows the response of one of these receptors to maintained transversal stretching of different amplitude (continuous line) and to a sinusoidal oscillation of the same maximal amplitude (dotted line, 1st.). It should be noted that for any given elongation the response to a varying stretch is greater, indicating that the receptor is not only sensing tension but also its rate of change. This property of the receptor does not have to be necessarily an intrinsic one but might very well be a reflection of the viscous properties of the microenvironment in which it is embedded. When we compare the first applied oscillation (dotted line) to one occurring a few cycles afterward (broken line) we see that the threshold for the receptor activation has increased and that, more

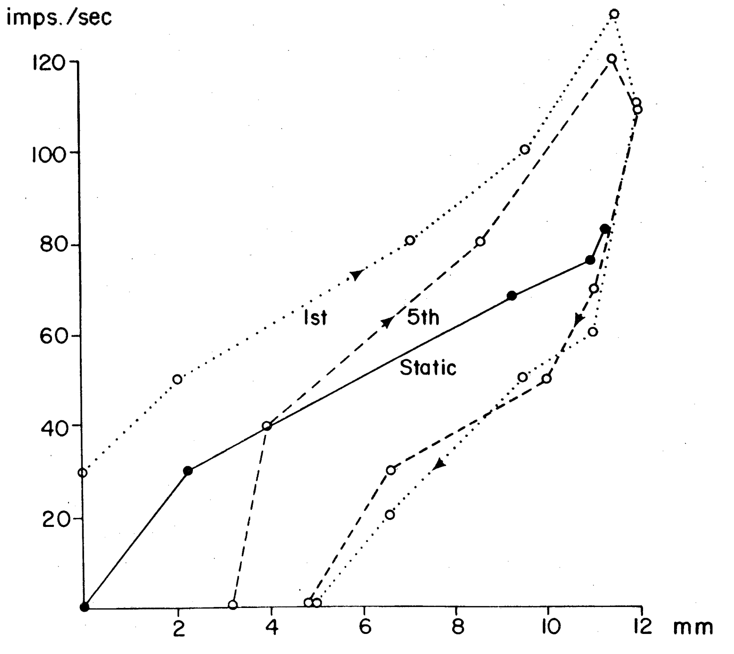

Fig. 2. – Response to transversal stretching of the posterior wall of a tracheal stretch receptor. The continuous line represents its response to maintained distensions (static), the dotted line its response during the first applied sinusoidal oscillation (1 st) and the broken line its response during the 5 th sinusoidal stretching (5 th).

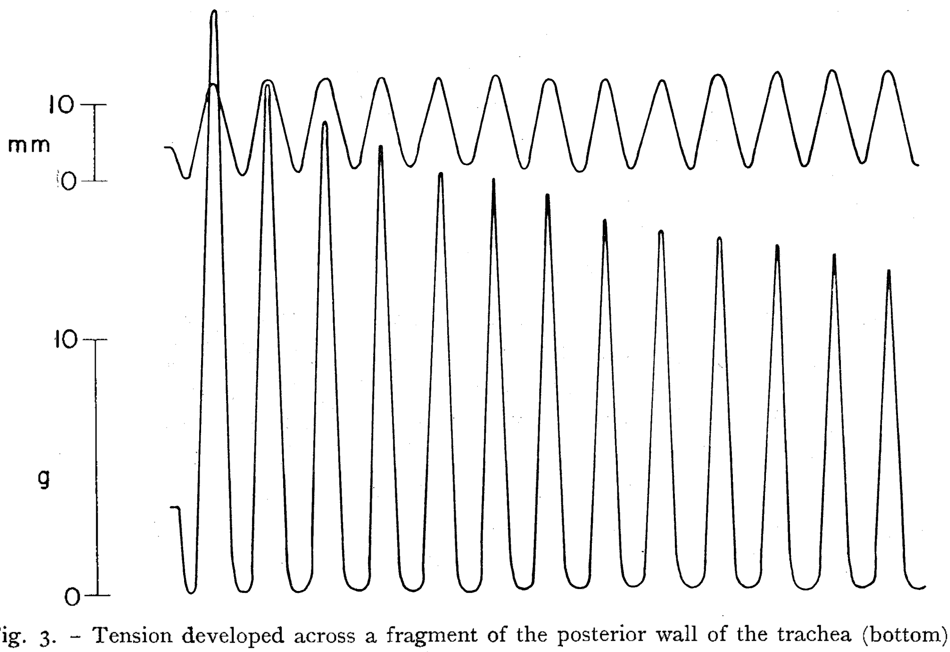

Fig. 3. – Tension developed across a fragment of the posterior wall of the trachea (bottom) during successive sinusoidal lengthening having constant amplitude (top). The tension decreases markedly in the first few oscillations.

generally, its response to elongation has decreased. This behavior can be explained examining the stress during successive oscillations of the back wall at constant strain (fig. 3): the tension decreases progressively during the first few oscillations. This should explain the greater response of the receptor to extension during the first cycle in which a greater force is developed for the same elongation. As mentioned in our previous study (Mortola and Sant'Ambrogio, 1977) the stress relaxation of the tracheal back wall is essentially due to the trachealis muscle.

Response to transmural pressure.

Fig. 4 represents the response of a tracheal stretch receptor to maintained distending and collapsing pressures (open circles, solid line). This behavior, which is representative of most of the tracheal stretch receptors, shows that

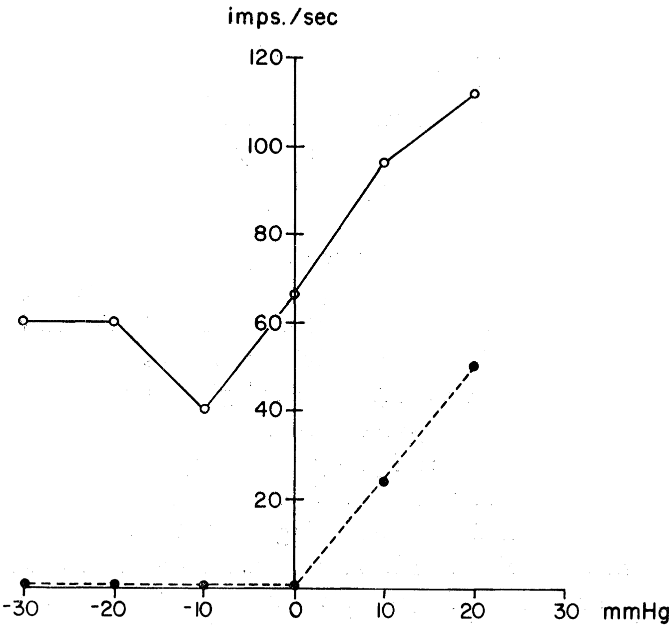

Fig. 4. – Response of a slowly adapting tracheal stretch receptor (imps/sec) to maintained positive and negative pressures without (open circles, solid line) and with transversal compression of the corresponding cartilagineous ring (closed circles, broken line).

the receptor is active at zero transmural pressure, i.e., at resting volume. This activity disappears when the cartilagineous ring, corresponding to the receptor site, is transversally compressed below its zero pressure position (solid circles, broken line). This fact indicates that the cartilagineous rings keep the posterior membraneous wall of the trachea stretched at zero transmural pressure.

The asymmetry of the response of the receptor to maintained positive and negative pressures could be explained on the basis of the fact that with negative transmural pressure the tension of the back wall depends on the balance between two conflicting factors: its inward stretching and the closing of the rings which tend to decrease the radius of curvature of the posterior wall and therefore its tension. With higher values of negative pressures the inward stretching of the posterior wall prevails because the cartilagineous rings become increasingly stiffer (Mortola and Sant'Ambrogio, 1977) and therefore the activity of the receptor increases. With lower values of transmural negative pressure the inward motion of the cartilagineous rings prevails leading to a decrease of the radius of curvature which, despite the increase of the pressure differential, lowers the tension of the posterior wall and hence the discharge of the receptor.

The response to positive transmural pressure after the cartilagineous rings have been fixed is lower (closed circles, broken line) than in the control situation. This could be attributed to the fact that the restraining of the cartilage abolishes its contribution to the stretch of the back wall at increasing values of pressures and to a smaller radius of curvature of the back wall at any transmural pressure.

The response to negative pressure after fixation of the cartilage is completely abolished and this might be interpreted by assuming that the back wall, having moved inward, is completely supported by the cartilage.

These findings indicate that the mechanical coupling between the cartilage and the back wall is the key factor in determining the behavior of these receptors. The asymmetry of their response to transmural pressure renders the slowly adapting receptors of the extrathoracic trachea capable of differentiating between inspiration (their activity decreases) and expiration (their activity increases). Had the supporting cartilagineous rings been completely rigid there would have been a symmetrical response to negative and positive transmural pressures and hence equally increasing signals would have originated during each of the two phases of the respiratory cycle.

Another consideration worth mentioning is that the structure of the trachea is also present in the main stem bronchi and the lobar bronchi (Vanpeperstraete, 1973). Since most of the stretch receptors (Miserocchi *et al.*, 1973; Miserocchi and Sant'Ambrogio, 1974) have been found to be located in these larger airways which during the forced expiration are downstream from the equal pressure point, it seems reasonable to assume that in this condition there might be some activation of the stretch receptors.

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