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The Diaphragm: Two Muscles

Abstract. *The costal and crural parts of the diaphragm were separately stimulated in anesthetized dogs. Stimulation of the costal part increased the dimensions of the lower rib cage, whereas stimulation of the crural part decreased the dimensions of the lower rib cage. It is concluded that the diaphragm consists of two muscles that act differently on the rib cage.*

The action of the diaphragm on the chest wall has been a source of interest to physiologists for centuries (*1*). When the diaphragm contracts, it pushes down on the viscera and displaces the abdomen outward. However, the mechanical link between the diaphragm and the rib cage remains poorly understood (*2*) and is a subject of active research because of the importance of this muscle (*3*).

Traditionally, the diaphragm has been thought to use the abdominal contents as a fulcrum to expand the rib cage (*1*, *2*). A recent quantitative description of this old idea suggests that the diaphragm can lift and expand the rib cage only to the extent that abdominal pressure increases (*4*). Thus, the proposed link between the diaphragm and the intercostal and accessory muscles of inspiration is that these two muscle groups, as pressure generators, operate on the rib cage as though they were arranged in series (*4*). However, recent observations in man, coupled with mathematical considerations, suggest that the diaphragm acts partly in series and partly in parallel with the rib cage (*5*). The present report demonstrates that this is indeed the case in the dog and, further, that these different actions of the diaphragm on the rib cage correspond to anatomically distinct parts of the muscle.

The studies were performed on supine dogs anesthetized with Nembutal (25 mg/kg), intubated, and maintained under deep general anesthesia with supplementary doses. The abdomen was opened and stimulating electrodes were implanted in the abdominal side of the diaphragm—two pairs in the costal part bilaterally and two pairs in the crural part bilaterally. They were placed as close as possible to the central tendon to avoid stimulation of other muscles. The abdomen was closed and the electrodes were connected to two Disa stimulators (Disamatic, Inc.) so that we could separately stimulate the costal and crural parts. The stimulating pulses were square waves 0.2 msec in duration and 20 to 100 Hz in frequency; the number of muscle fibers activated was set by progressively increasing the voltage. We measured air flow and volume at the animal's mouth with a Fleisch pneumotachograph. Transabdominal pressure was measured as the difference between the abdominal and atmospheric pressures. Changes in lower rib cage and abdominal dimensions were determined by induction plethysmography (*6*).

Representative records are shown in Fig. 1. Electrical stimulation of the costal part of the diaphragm resulted in increases in lung volume and abdominal pressure and in outward displacement of the abdomen and lower rib cage; expansion of the lower rib cage increased as the stimulation became stronger. On the other hand, stimulation of the crural part, while also producing increases in lung volume, abdominal pressure, and abdominal dimensions, had no effect on lower rib cage dimensions. This was true for any amplitude of stimulation. Similar records were obtained for all the dogs studied.

In order to suppress the role played by the increase in abdominal pressure on the changes in rib cage dimensions, we repeated the procedure with the abdomen opened. Stimulation of the costal part of the diaphragm still displaced the rib cage outward, although less markedly than with the abdomen closed. By contrast, stimulation of the crural part re-

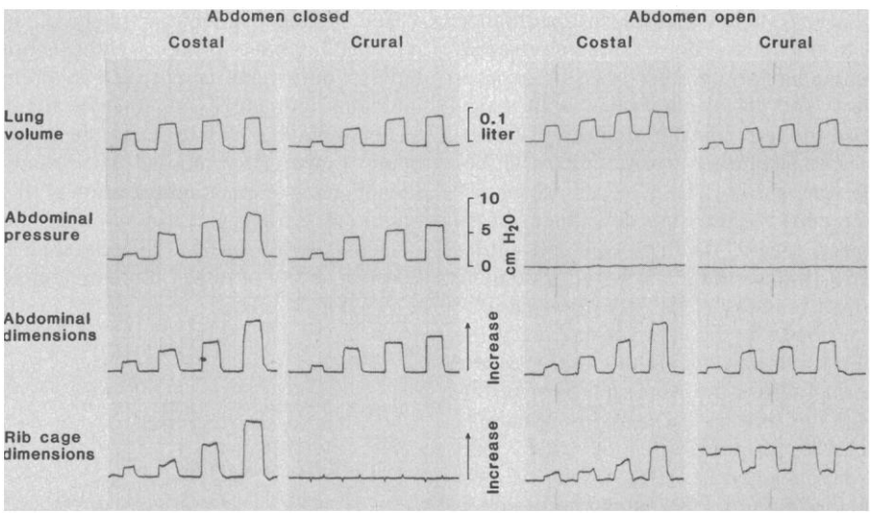

Fig. 1. Effect of stimulating the costal and crural parts of the diaphragm on lung volume, abdominal pressure, and abdominal and rib cage dimensions. The stimulation frequency was 100 Hz, and in each panel the voltage of the stimulation increased from left to right.

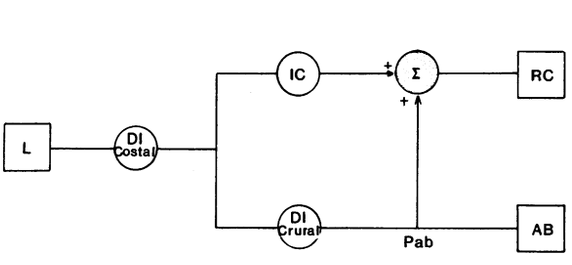

Fig. 2. Schematic diagram of the muscular control of the respiratory system. The squares represent structures (*L*, lungs; *RC*, rib cage; *AB*, abdomen) which are displaced by muscles, represented as circles (*DI*, diaphragm; *IC*, intercostal and accessory muscles of inspiration). Σ is a summing junction; *Pab* is the change in abdominal pressure resulting from diaphragmatic contraction.

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sulted in paradoxical (inward) displacement of the lower rib cage. The displacement was increased by increasing the amplitude of the stimulus.

Our data clearly indicate that in dogs the diaphragm consists of two muscles that act differently on the rib cage. The costal part of the muscle has a direct inspiratory action on the lower rib cage, even without the aid of increase in abdominal pressure. This is consistent with the arrangement of these fibers, which are inserted into the ribs and directed upward, parallel to the rib cage. On the other hand, the crural part has an expiratory action on the lower rib cage as long as abdominal pressure is not able to increase. These fibers have no insertion on the ribs, and their expiratory effect on the rib cage could be due to the fall in pleural pressure or to a force directed inward and backward. This force would be transmitted to the ribs through the central tendon and costal fibers and would diminish the area of apposition between the costal fibers and the rib cage. In the intact animal the expiratory effect of the crural diaphragm is balanced by the rise in abdominal pressure (Fig. 1).

Figure 2 illustrates a model of a respiratory system behaving in accordance with our data. The diaphragm is represented as two different pressure generators. The costal diaphragm is in series with the intercostal and accessory muscles of inspiration, while the crural diaphragm is in parallel. The summing junction adds the pressure developed across the rib cage by the intercostal and accessory muscles to the change in abdominal pressure and to the pressure directly developed by the contracting part of the diaphragm, producing the total pressure acting across the rib cage. As a result, with the intercostal muscles remaining relaxed, contraction of the crural part would have no net effect on the rib cage if the gain at the summing junction adjusted the change in abdominal pressure so that it was exactly equal and opposite to the change in pleural pressure. On the other hand, contraction of the costal part would expand the rib cage through a direct effect and through the increase in abdominal pressure.

The model of the diaphragm as two separate muscles, one in series, the other in parallel with the rib cage, has a clear anatomical counterpart. It also has an embryological counterpart. The muscular portion of the diaphragm does not arise as a single sheet, but as individual muscle bundles. This is true both in the phylogeny of animal species (*7*) and in man, where the costal part of the diaphragm develops from myoblasts originating in the lateral body walls while the crural part develops in the dorsal mesentery of the esophagus (*8*). These two parts of the diaphragm also differ from each other in terms of fiber composition (*9*) and nerve root innervation (*10*). We have now established that the costal and crural parts have different actions on the chest wall.

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Chloramphenicol Administration During Brain Development: Impairment of Avoidance Learning in Adulthood

Abstract. *Rats treated with chloramphenicol from days 7 to 21 of intrauterine life (50 milligrams per kilogram per day, injected subcutaneously into the mothers) or in the first 3 days of extrauterine life (50 to 100 milligrams per kilogram per day) were trained for avoidance conditioning when 60 days old. The acquisition of the avoidance response was impaired to a highly significant degree in all the treated groups.*

The finding that chloramphenicol, in mammals, inhibits protein synthesis not only in mitochondria but also in brain junctional complexes at concentrations easily attainable with doses in the therapeutic range (*1*), prompted us to study the influence of the administration of this antibiotic during pregnancy or in the neonatal period on the later avoidance learning ability of rats. Chloramphenicol is still widely used in Europe and many Latin countries as a broad-spectrum antibiotic. Our results show that avoidance learning is impaired in rats exposed to chloramphenicol during brain development.

Wistar female rats, 3 months old (Morini, S. Polo d'Enza, Reggio Emilia, Italy), given free access to food, were timemated and thereafter placed in separate cages. The rats were assigned at random to four groups of 15. The date of concep-

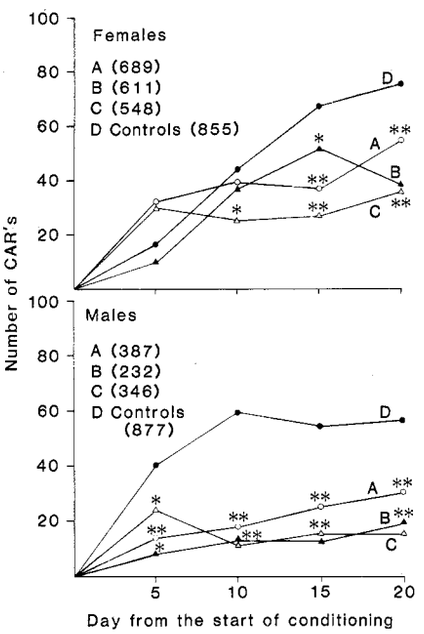

Fig. 1. The effect of early treatment with chloramphenicol on avoidance conditioning in rats (60 days old). The graphs show the number of conditioned avoidance responses (CAR's) on days 5, 10, 15, and 20 after the start of conditioning; each rat was given ten trials per day and there were ten rats in each group. Curve A: the rats had received chloramphenicol (50 mg/kg-day) from days 7 to 21 of intrauterine life. Curves B and C: rats in these groups had received chloramphenicol (50 or 100 mg/kg-day, respectively) for the first 3 days of extrauterine life. Numbers in parentheses show the number of CAR's achieved by each group during the whole period of conditioning (20 consecutive days: 2000 trials per group). Difference from controls: *, $P < .05$; **, $P < .001$ (the number of CAR's achieved by the treated groups on days 5, 10, 15, and 20 of conditioning, as well as the total number of CAR's during the whole period of conditioning were compared with the corresponding values of the control groups by the χ^2 test).

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