

Vector analysis in partitioning of inspiratory muscle action in dogs

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ABSTRACT: We considered the displacements and the pressure changes resulting from isolated contraction of 2 muscles as analogous to 2 vectors and those during simultaneous contraction as resultants. These were resolved into contributing components to calculate the contribution of each muscle group and partition the action of inspiratory muscles. Relative displacements of rib cage (ΔRC) and abdomen (ΔAB) and changes in transpulmonary (ΔPL) and abdominal (ΔPab) pressures were obtained during spontaneous breathing, isolated contraction of rib cage muscle (RCM), diaphragmatic (DI), costal and crural diaphragm and passive inflation in 7 dogs.

The diaphragm accounted for $58 \pm 19.8\%$ SD of the chest wall displacement and $90 \pm 6.6\%$ SD of the pressure swings during spontaneous breathing. The costal diaphragm accounted for $61 \pm 28.9\%$ SD of the displacement produced by contraction of the entire diaphragm. Despite wide variability in the action of the diaphragm and its components, all animals breathed close to their relaxation characteristic.

We conclude that there are marked differences in the degree of RCM recruitment between dogs in order to prevent chest wall distortions.

Eur Respir J., 1992, 5, 219-227.

We present a method of partitioning the respiratory displacements and pressure swings accompanying inspiratory muscle contraction among the contributing muscle groups in dogs. This analysis is used to calculate the following parameters:

1. The diaphragmatic and rib cage muscle contribution to the chest wall displacements and inspiratory pressure changes during spontaneous breathing;
2. The contributions of the costal and crural part of the diaphragm to the resultant chest wall displacement during contraction of the entire diaphragm;
3. The contribution of the insertional component to the action of the costal part and of the entire diaphragm.

Rationale

When lower rib cage and abdominal displacements are plotted against each other during a spontaneous inspiration the slope of the relationship is the result of the simultaneous actions of the diaphragm and the rib cage muscles. The actions of these two muscle groups are different. The diaphragm expands the lower rib cage and displaces the abdomen outward. The rib cage muscles also expand the lower rib cage but displace the abdomen inward. When both muscle groups contract

simultaneously the displacements are in between these extremes. Similarly, diaphragmatic contraction causes both transpulmonary (PL) and abdominal (Pab) pressures to increase, while (in the absence of passive tension in the diaphragm) rib cage muscle contraction causes Pab to fall by an amount equal to the increase in PL. Simultaneous contraction of both muscle groups again results in a slope of the $\Delta PL/\Delta Pab$ relationship which falls somewhere between the slopes which occur when either muscle contracts alone.

Provided that: 1) the rib cage and abdomen move independently; 2) PL and Pab change independently; and 3) contraction of one muscle group does not alter the action of the other, then the displacements and pressure changes which accompany the isolated contraction of two inspiratory muscle groups are analogous to two vectors and have both direction and magnitude. The displacements and pressure changes during the simultaneous contraction of these two muscle groups may be considered as the resultant of the two contributing vectors. If the directions of the vectors and their resultant is known it is possible to calculate the contributions of each muscle group to both the magnitude and direction of the resultant.

This provides a graphical method to solve the equation:

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Keywords: Chest wall displacement
costal
crural
diaphragm
respiratory muscles.

Received: December 31, 1990; accepted
after revision September 9, 1991.

Supported by a contract with the Ministere
de la Politique Scientifique (Science de la
Vie) of Belgium, the MRC of Canada and
the E/L JTC Fund.

$$\Delta RC = (ax + b(1-x)) \cdot \Delta AB$$

Where ΔRC is the displacement of the rib cage, ΔAB is the abdominal displacement, a is the coefficient of proportionality between ΔRC and ΔAB during diaphragm contraction, b is that during rib cage muscle contraction and x is the fractional contribution of the diaphragm to the partitioning ($1 > x > 0$).

A similar analysis applies to the separate contributions of the costal and crural parts of the diaphragm as well as to the contribution of the "insertional" and "noninsertional" components to the overall action of the diaphragm when it contracts as a whole.

Methods

Studies were performed on 7 mongrel dogs (16–25 kg) in the supine position anaesthetized with sodium pentobarbital (initial dose 25 mg·kg⁻¹). The dogs were intubated with cuffed endotracheal tubes and intravenous cannulae were inserted in order to administer supplementary doses of anaesthetic as needed to maintain absence of the corneal reflex. Flow through the endotracheal tube was measured using a pneumotachograph (Fleisch No. 2) and differential pressure transducer (HP 270±4 cmH₂O). The flow signal was electronically integrated to yield the change in lung volume (ΔV_L). An electrode tipped stimulating catheter was inserted through the left external jugular vein and advanced until stimulation resulted in symmetrical contraction of the diaphragm without contraction of the muscles of the upper limb or rib cage. The diaphragm was exposed through a long midline abdominal incision. Stainless steel hook stimulating electrodes were inserted and anchored 1–2 cm apart in the muscular fibres of the crural diaphragm and in the costal diaphragm as close as possible to the central tendon.

Isolated contraction of each part of the diaphragm during costal and crural stimulation and symmetrical contraction of the entire diaphragm during transvenous phrenic nerve stimulation were confirmed by direct visualization prior to closure of the abdomen. A catheter-balloon system and differential pressure transducers (Validyne DP 15 ±100 cmH₂O) were used to measure pressure in the mid-oesophagus and under the dome of the right hemidiaphragm to estimate P_L and P_{ab} , respectively. The abdomen was sutured and residual intra-abdominal air was evacuated through a catheter placed in the epigastrium through the abdominal incision. Continuous evacuation of accumulated oesophageal fluid was provided by a suction catheter placed just above the oesophageal balloon.

Abdominal and lower rib cage displacements were measured using inductance plethysmography (Respirace[®], Ambulatory Monitoring Inc.). The abdominal respiband was placed just caudal to the umbilicus. The band used to record rib cage displacement was placed around the lower rib cage over the zone of apposition of the diaphragm (determined by percussion) and positioned such that the middle of the band width

overlay the end of the xiphoid process. The Respirace gains were set such that an isovolume manoeuvre (performed by manual deflation of the rib cage during airway occlusion) resulted in equal and opposite signals for rib cage and abdominal displacements.

All measurements were recorded on a strip chart recorder (Graptect WR 3101). Rib cage (ΔRC) and abdominal (ΔAB) displacements were also displayed on the abscissa and ordinate of a storage oscilloscope screen (Tektronix 5111).

All stimulations were performed at functional residual capacity (FRC) during apnoea induced by hyperventilation using a Medelec SC6 stimulator (frequency 50–100 Hz, duration 2 ms). The stimulation voltage was adjusted so that the resulting displacements of the rib cage and abdomen were within the range observed during quiet breathing. Under each condition 5–10 stimulations resulting in roughly equal chest wall displacement were selected for analysis and the mean values for each condition were used to calculate the direction of the corresponding vector. Measurements were performed during isolated costal stimulation, isolated crural stimulation, transvenous phrenic nerve stimulation, passive inflation (to obtain the relaxation characteristics) and spontaneous breathing.

Analysis

We measured or calculated the directions of the following vector pairs and their resultants:

1. The displacement vectors during isolated diaphragmatic contraction, isolated rib cage muscle contraction (calculated, see below) and their resultant during spontaneous breathing;
2. The pressure vectors representing isolated diaphragmatic contraction, isolated rib cage muscle contraction (calculated, see below) and their resultant during spontaneous breathing;
3. The displacement vectors measured during separate costal and crural stimulation and the resultant during phrenic nerve stimulation;
4. The displacement vectors representing the insertional component (driving the chest wall along its relaxation characteristic) and noninsertional component (direction identical to isolated crural contraction) of diaphragm action and their resultants during contraction of the costal part and of the entire diaphragm.

During a spontaneous breath the rib cage moves, approximately, as a single compartment [1, 2]. In addition, the diaphragm contracts and shortens to a length at which no passive tension would be expected [3]. In calculating the contributions of the rib cage muscles and diaphragm to the spontaneous breathing resultants it is necessary to determine the slope of the $\Delta P_L/\Delta P_{ab}$ and $\Delta RC/\Delta AB$ relationships which would be observed if the rib cage muscles contracted alone under the same conditions which prevail during spontaneous breathing. Since phrenicotomy does not mimic these conditions [1] these theoretical slopes must be calculated.

When the inspiratory muscles of the rib cage contract alone in the absence of passive transdiaphragmatic pressure (Pdi) the change in PL is equal and opposite to the change in Pab. The slope of the $\Delta P_L/\Delta P_{ab}$ relationship under these conditions is therefore -1.

When the rib cage and abdomen each move with a single degree of freedom, as is approximately the case during quiet breathing, the change in each compartment's volume (ΔV_{rc} and ΔV_{ab}) is proportional to its displacement. The slope of the $\Delta RC/\Delta AB$ relationship is therefore equal to the ratio of the volume displaced by each compartment ($\Delta V_{rc}/\Delta V_{ab}$). Since the change in lung volume equals the change in rib cage volume plus the change in abdominal volume:

$$\Delta V_{rc} = V_L - \Delta V_{ab} \quad (1)$$

Dividing both sides of equation (1) by ΔV_{ab} yields:

$$\Delta V_{rc}/\Delta V_{ab} = \Delta V_L/\Delta V_{ab} - 1 \quad (2)$$

However, $\Delta V_L = \Delta P_L \cdot C_L$ and $\Delta V_{ab} = \Delta P_{ab} \cdot C_{ab}$ where C_L and C_{ab} are the compliances of the lung and abdomen, respectively, and ΔP_L and ΔP_{ab} are taken at points of zero flow. Therefore:

$$\Delta V_{rc}/\Delta V_{ab} = (\Delta P_L \cdot C_L) / (\Delta P_{ab} \cdot C_{ab}) - 1 \quad (3)$$

During isolated rib cage muscle contraction in the absence of passive Pdi, $\Delta P_L = -\Delta P_{ab}$. Therefore, equation (3) simplifies to:

$$\Delta V_{rc}/\Delta V_{ab} = -C_L/C_{ab} - 1 \quad (4)$$

C_L was calculated as $\Delta V_L/\Delta P_L$ measured between the points of zero flow at end-expiration and end-inspiration. The change in abdominal volume was calculated as follows:

$$\Delta V_{ab} = \Delta V_L \cdot \Delta AB / (\Delta AB + \Delta RC) \quad (5)$$

where ΔAB and ΔRC are the magnitudes of the respitrace signals for abdomen and rib cage, respectively. The abdominal compliance was then calculated as $\Delta V_{ab}/\Delta P_{ab}$ measured between the points of zero flow at end-expiration and end-inspiration. The values of C_L and C_{ab} used in calculation of $\Delta RC/\Delta AB$ during isolated rib cage muscle contraction represent the means measured during 10 consecutive spontaneous breaths.

Sample calculations in one representative animal (dog 1) are presented in figures 1-7. In figure 1, rib cage displacement (ΔRC) is plotted on the y-axis with abdominal displacement (ΔAB) on the x-axis. The displacements during spontaneous breathing (SB) represent the resultant of two contributing vectors, RCM representing isolated rib cage muscle contraction and PHR representing isolated diaphragmatic contraction. For any given magnitude of SB the relative magnitudes of the two contributing vectors may be calculated by constructing the parallelogram depicted. Projecting each

vector onto the resultant, by constructing perpendiculars through the ends of the contributing vectors allows calculation of the relative contributions to the magnitude of the resultant (the distance OC). In the example in figure 1 the distance OA is the contribution of the rib cage muscles and OB is the contribution of the diaphragm.

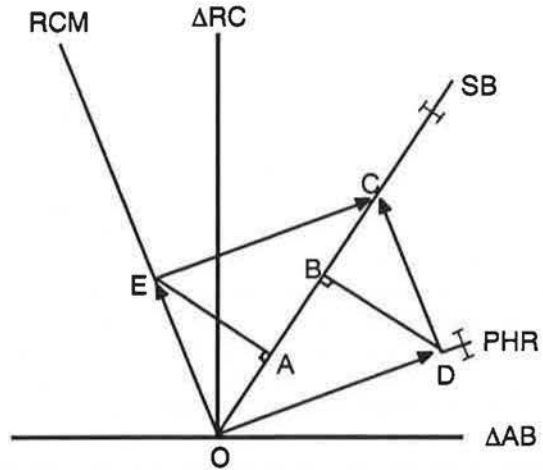


Fig. 1. - Partitioning of displacements during spontaneous breathing. SB represents the resultant displacements during spontaneous breathing. The contributing vectors, RCM and PHR, represent the relative displacements during isolated rib cage muscle contraction and isolated diaphragmatic contraction, respectively. The contribution of the rib cage muscle vector to the magnitude of the resultant is given by the distance OA and that of the diaphragm is given by the distance OB. Error bars indicate standard errors of the slopes.

An index of the influence of each vector on the direction of the resultant is provided by the ratio of the magnitudes of the two vectors. In the example in figure 1, the angle between the PHR vector and the resultant is less than that between the RCM vector and resultant, indicating that the diaphragm has a greater influence on the direction of the resultant (relative displacements of rib cage and abdomen) during a spontaneous breath than the rib cage muscles. This is reflected in the ratio of the magnitude of the diaphragmatic vector to that of the rib cage muscle vector (OD/OE). Because BD=EA, the ratio of the sine of the angle EOC to that of the angle DOC given by (EA/OE)/(BD/OD) = OD/OE. Thus, the ratio of the magnitude of the vectors determines the direction of the resultant relative to the direction of its component vectors.

The influence of a vector on the direction of the resultant can be quite different from its contribution to the magnitude. For example, a vector which forms an angle of 90° with the resultant contributes little to its magnitude but may have a major influence on its direction. As will be seen, this was the case when comparing the influence of diaphragm and rib cage muscles on the magnitude and direction of the resulting changes in PL and Pab.

Vector analysis can also determine whether two muscle groups are synergistic or antagonistic. When muscle action is synergistic the magnitude of the

resultant is greater than the magnitude of either of the vectors, *i.e.* each vector contributes positively to the magnitude of the resultant. The opposite (antagonistic action) occurs when the angle between a vector and the resultant is greater than 90° .

In figure 2 the contributing vectors are projected onto the x and y axes in order to calculate their contributions to the net displacement in each dimension during their simultaneous contraction. Here we distinguish between distance and displacement. The latter can be positive or negative depending on direction. The distance travelled, however, is always positive and is independent of direction. In this example the total displacement along the rib cage (ΔRC) axis is the distance OI . The contribution of the RCM vector to rib cage displacement is the distance HI and that of the PHR vector is OH . To calculate the relative contributions to abdominal displacement the vectors are projected onto the abdominal (ΔAB) axis. The displacement along this axis during isolated RCM contraction is FG and is negative. During isolated diaphragmatic contraction the displacement is OF and is positive. The net displacement along this axis is equivalent to a distance "travelled" by the abdominal wall first outward from O to F then inward, a distance equal to FG , to arrive at a final net displacement equal to OG . The total distance travelled by the abdominal wall, therefore, is the sum of the distances OF and FG . Note that even though the directions of these distances are opposite, (that is, the rib cage muscles and diaphragm are antagonistic in their action on the abdominal wall), the rib cage muscle contribution to the resultant displacement along this axis is still given by the distance FG and that of the diaphragm by the distance OF .

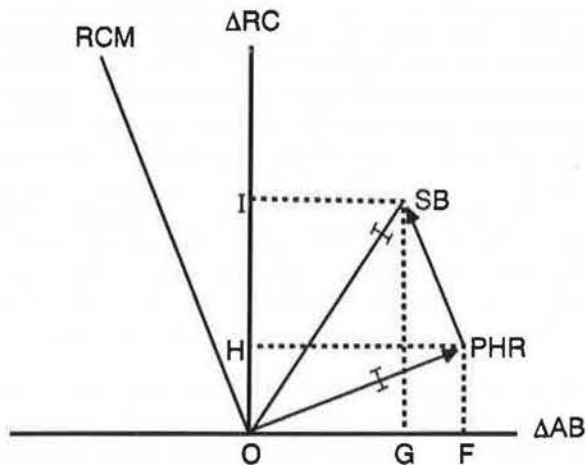


Fig. 2. - Calculation of diaphragmatic contributions to rib cage displacement (ΔRC) and abdominal displacement (ΔAB) during spontaneous breathing. SB is the resultant displacement during spontaneous breathing. RCM and PHR are vectors representing the relative displacements during isolated rib cage and diaphragmatic contraction, respectively. The rib cage muscle contribution to ΔRC is given by the distance HI and that of the diaphragm is given by the distance OH . The rib cage muscle contribution to ΔAB is given by the distance FG and the diaphragmatic contribution to ΔAB is given by the distance OF . Error bars indicate standard errors of the slopes.

A similar analysis was used to partition the inspiratory pressure swings during spontaneous breathing. In figure 3 the change in transpulmonary pressure (ΔP_L) is plotted on the y-axis against the change in abdominal pressure (ΔP_{ab}) on the x-axis. During spontaneous breathing the relative changes in these pressures are given by the slope of SB . The vector RCM represents the pressure swings during isolated rib cage muscle contraction in the absence of passive tension in the diaphragm and PHR represents those during isolated diaphragmatic contraction. As with the displacement vectors, construction of perpendiculars to the resultant through the ends of the contributing vectors allows calculation of their relative magnitudes. OA represents the contribution of RCM and OB represents the contribution of the diaphragm to the pressure swings during spontaneous breathing. The ratio OD/OE gives the relative influence of the diaphragm and rib cage muscles to the direction of the spontaneous breathing vector.

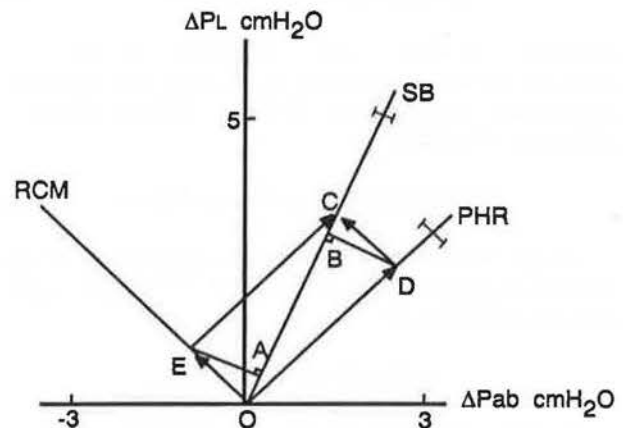


Fig. 3. - SB represents the resultant change in transpulmonary pressure (ΔP_L) and abdominal pressure (ΔP_{ab}) during spontaneous breathing. RCM and PHR are vectors representing the relative changes in P_L and P_{ab} during isolated rib cage muscle and isolated diaphragmatic contraction, respectively. OA is the contribution of the rib cage muscles and OB is the contribution of the diaphragm. Error bars indicate standard errors of the slopes.

In figure 4 the contributing pressure vectors (RCM) and PHR are projected onto the ΔP_L and ΔP_{ab} axes in order to calculate their contribution to the change in each of these pressures.

In figure 5 the resultant displacement during diaphragmatic contraction (PHR) is resolved into its two contributing vectors, COS representing the displacements during isolated contraction of the costal part and CRU representing the displacements during isolated crural contraction.

In figure 6 the action of the costal part of the diaphragm is partitioned into its insertional and noninsertional components. Since the crural diaphragm has no anatomical insertion on the lower rib cage, the direction of the vector representing the noninsertional action of the costal part ($NONINS$) is identical to that during isolated crural contraction. The direction of the vector representing the insertional component (INS) of the action of the costal part is the same as that during passive inflation (see discussion).

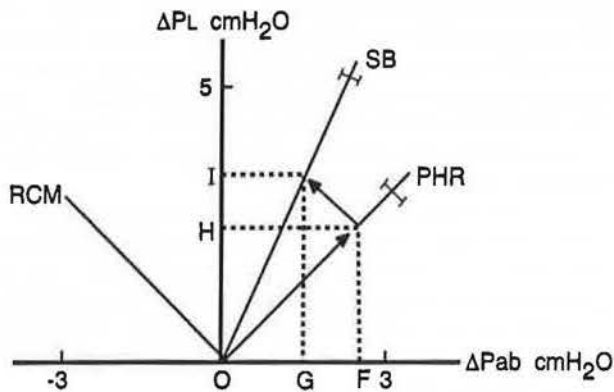


Fig. 4. - The changes in transpulmonary pressure (ΔP_l) and abdominal pressure (ΔP_{ab}) during spontaneous breathing are partitioned into the contributions of the rib cage muscles and diaphragm by projecting their corresponding vectors onto the ΔP_l and ΔP_{ab} axes. The rib cage muscle contribution to ΔP_l is given by the distance HI and the diaphragmatic contribution is given by the distance OH. The contribution of the rib cage muscle vector to ΔP_{ab} is given by the distance FG and the diaphragmatic contribution to ΔP_{ab} is given by the distance OF. Error bars indicate standard errors of the slopes.

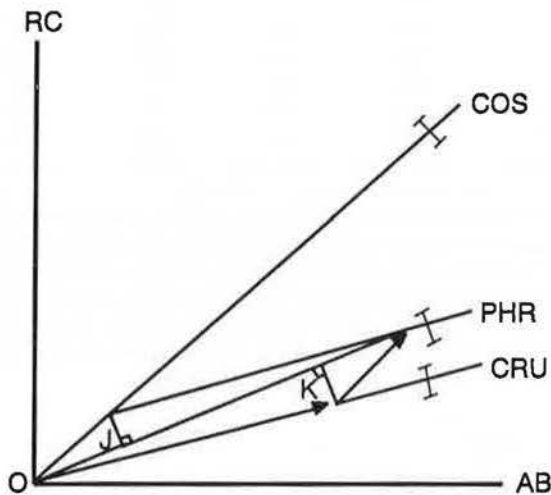


Fig. 5. - The action of the diaphragm is partitioned into the contributions of its costal and crural parts. PHR represents the relative displacements of the rib cage (ΔRC) and abdomen (ΔAB) during contraction of the entire diaphragm. The contributing vectors COS and CRU represent the relative displacements during isolated contraction of the costal and crural parts, respectively. The distance OJ is the contribution of the costal part and OK is the contribution of the crural part. Error bars indicate standard errors of the slopes.

In figure 7, PHR represents the resultant displacement during contraction of the entire diaphragm. The vector INS represents the insertional action of the diaphragm (direction identical to that during passive inflation) and the vector NONINS represents the noninsertional action (direction identical to isolated crural contraction). The relative contributions of the insertional and noninsertional components to the magnitude and direction of diaphragmatic action are calculated by construction of the depicted parallelogram and perpendiculars and from the ratio of the magnitudes of the contributing vectors.

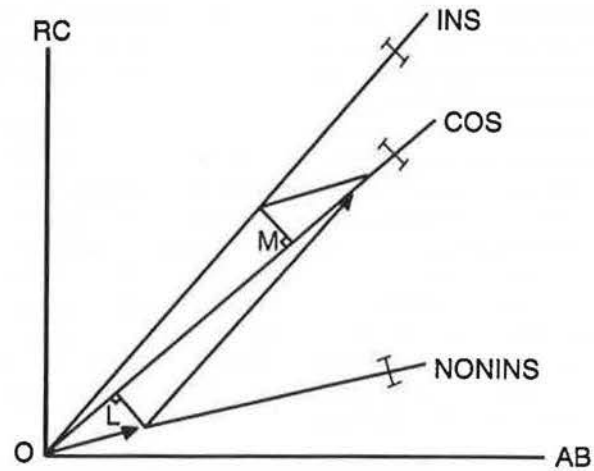


Fig. 6. - Calculation of the insertional and noninsertional components of costal action. COS, represents the resultant displacements during contraction of the entire costal part. INS is the vector representing the insertional component of diaphragmatic action (direction identical to that during passive inflation) and NONINS is the vector representing its noninsertional action (direction identical to that during isolated crural contraction). The contribution of the insertional component is given by the distance OM and that of the noninsertional component is given by the distance OL. Error bars indicate standard errors of the slopes.

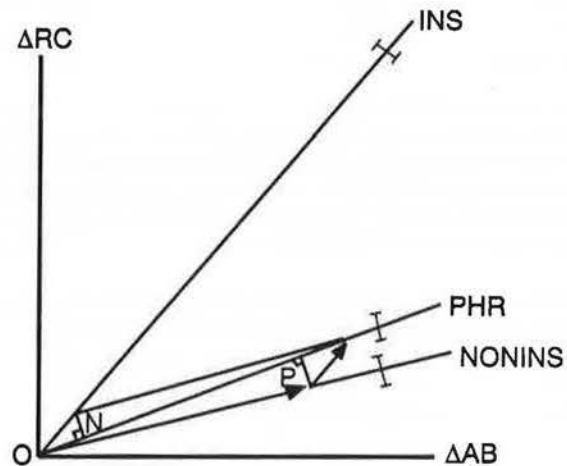


Fig. 7. - The action of the diaphragm is partitioned into its insertional and noninsertional components. The vector INS represents the insertional action of the diaphragm (direction identical to that during passive inflation). The vector NONINS represents the noninsertional action of the diaphragm (direction identical to isolated crural contraction). The contribution of the insertional component of the diaphragm is given by the distance ON and the contribution of the noninsertional component is the distance OP. Error bars indicate standard error bars of the slopes.

Our analysis assumes linearity. This is valid for small displacements and pressure changes, however, the results only apply to small volume changes above supine FRC.

Results

Confirming the work of the others [1, 4] we found that all dogs breathed spontaneously on or very close to the relaxation characteristic. In all animals the

diaphragm and rib cage muscles were synergistic in that in all cases the magnitude of the spontaneous breathing resultant was always greater than the magnitude of either of the contributing vectors.

Tables 1 and 2 present the diaphragmatic contributions to the magnitudes of the resultant chest wall displacements and respiratory pressure swings during spontaneous breathing and the ratios of the magnitudes of the diaphragmatic and rib cage muscle (RCM) vectors which determine the direction of the resultants during spontaneous breathing. The diaphragmatic contributions to the magnitude of the resultant displacements (mean \pm SD, 58 \pm 19.8%) and to the direction of the resultants (1.50 \pm 0.97) were highly variable between animals.

Table 1. — Diaphragmatic contributions to resultant displacements during spontaneous breathing

Dog No.	DI contribution to magnitude of SB %*	DI/RCM**
1	66	1.38
2	25	0.49
3	81	2.70
4	40	0.73
5	50	0.95
6	84	2.92
7	59	1.30
Mean \pm SD	57.9 \pm 19.8	1.50 \pm 0.97

DI: vector representing relative displacements of rib cage and abdomen during isolated diaphragmatic contraction; SB: resultant displacements during spontaneous breathing; DI/RCM: ratio of magnitudes of the contributing diaphragmatic and rib cage muscle vectors. *: equivalent to OB/OC in figure 1; **: equivalent to OD/OE in figure 1.

Table 2. — Diaphragmatic contributions to resultant pressure changes during spontaneous breathing

Dog No.	DI contribution to magnitude of SB %	DI/RCM
1	87	2.50
2	96	3.10
3	97	3.59
4	98	7.40
5	84	1.53
6	80	1.47
7	87	2.03
Mean \pm SD	89.9 \pm 6.6	3.09 \pm 1.9

DI: vector representing relative changes in transpulmonary and abdominal pressure during isolated diaphragmatic contraction; SB: resultant pressure changes during spontaneous breathing; DI/RCM: ratio of magnitudes of contributing diaphragmatic and rib cage muscle vectors.

The diaphragmatic contribution to the resultant pressure change (mean \pm SD, 90 \pm 6.6%) has a smaller standard deviation than that for its contribution to chest wall displacement. This is the necessary result of the fact that the diaphragmatic contribution was much greater than that of the rib cage. Large interanimal variability was, however, observed in the relative magnitudes of

the contributing diaphragmatic and RCM vectors (DI/RCM) (e.g. dog 4 vs dogs 5 and 6). This is because the angle between the RCM vector and the resultant approached 90° in all animals (compare figures 1 and 3). Therefore, while changes in magnitude of the RCM pressure vector altered the direction of the resultant they had little effect on its magnitude.

Table 3 presents the diaphragmatic contribution to ΔP_L , ΔP_{ab} , ΔRC and ΔAB during spontaneous breathing. The diaphragmatic contribution to ΔP_{ab} was not significantly different (paired t-test) from its contribution to ΔAB (fig. 8). In contrast, no correlation was found between the diaphragmatic contribution to ΔP_L and its contribution to RC.

Table 3. — Diaphragmatic contributions to changes in transpulmonary and abdominal pressures and to rib cage and abdominal displacements during spontaneous breathing

Dog No.	ΔP_{Ldi} %	ΔP_{abdi} %	ΔRC_{di} %	ΔAB_{di} %
1	70	73	35	78
2	70	79	16	71
3	74	80	60	80
4	79	82	29	74
5	36	67	35	73
6	42	66	72	78
7	50	75	62	71
Mean \pm SD	62 \pm 15.4	76 \pm 15.4	42 \pm 17.9	74 \pm 6.2

ΔP_{Ldi} : diaphragmatic contribution to the change in transpulmonary pressure during spontaneous breathing; ΔP_{abdi} : diaphragmatic contribution to the change in abdominal pressure during spontaneous breathing; ΔRC_{di} : diaphragmatic contribution to rib cage displacement during spontaneous breathing; ΔAB_{di} : diaphragmatic contribution to abdominal displacement during spontaneous breathing.

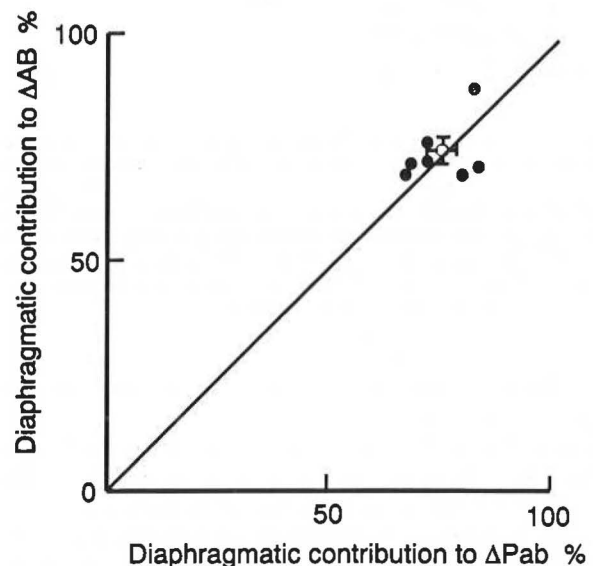


Fig. 8. — The diaphragmatic contribution to the change in abdominal pressure during spontaneous breathing is plotted on the x-axis against the diaphragmatic contribution to the abdominal displacement during spontaneous breathing on the y-axis. The points do not deviate significantly from the line of identity. Error bars indicate standard errors of the slopes.

Table 4 presents the costal contribution to the resultant displacements during isolated diaphragmatic contraction (mean \pm SD, 61 \pm 29.9%), and the contribution of the insertional component to the action of the costal part (66 \pm 27.9%) and to the action of the entire diaphragm (37 \pm 24.7%). Both the contribution of the costal part and the contribution of the insertional component to the action of the diaphragm varied widely among dogs, however, there was no significant correlation between these two parameters. The variability in the insertional component is therefore not entirely explained by differences in the predominance of the costal action.

Table 4. - Partitioning of diaphragmatic action

Dog No.	COS/DI %	INS/COS %	INS/DI %
1	25	75	22
2	16	85	11
3	73	96	69
4	92	29	26
6	89	83	74
7	73	25	21
Mean \pm SD	61.3 \pm 29.9	65.5 \pm 27.9	37.1 \pm 24.7

COS/DI: costal contribution to resultant displacement during contraction of the entire diaphragm; INS/COS: contribution of insertional component of costal action to displacements during contraction of the costal part; INS/DI: contribution of insertional action to displacements during contraction of the entire diaphragm. In dog No. 5 isolated contraction of the crural part could not be achieved therefore partitioning of diaphragm action could not be accomplished.

The diaphragmatic contribution to the resultant displacements during spontaneous breathing correlated significantly with the insertional component of diaphragmatic action ($r=0.84$, $p<0.001$, fig. 9). In other words, the further the diaphragm displaced the rib cage and abdomen away from the relaxation characteristics the more the rib cage muscles were recruited to restore this relationship. In those animals in which the diaphragmatic contribution to the displacements during spontaneous breathing was small, either the crural part dominated diaphragmatic action (dog No. 2) or the costal part displaced the rib cage and abdomen far from their relaxation characteristic (*i.e.* the insertional component of costal action was small; *e.g.* dog No. 4). In dog No. 7, which also had a small insertional component (21%) the diaphragmatic contribution to the displacements during spontaneous breathing was important (59%). In this animal, the crural part had an important inflationary action on the lower rib cage and the angle between the costal and crural vectors was small (10.5°). Thus, even though the insertional component of diaphragmatic action was small, the diaphragmatic vector was not far from the spontaneous breathing resultant. In those animals in which the diaphragmatic contribution to spontaneous breathing was large (dogs No. 3 and 6), the costal part dominated diaphragmatic action and the insertional component was the largest among all of the dogs studied.

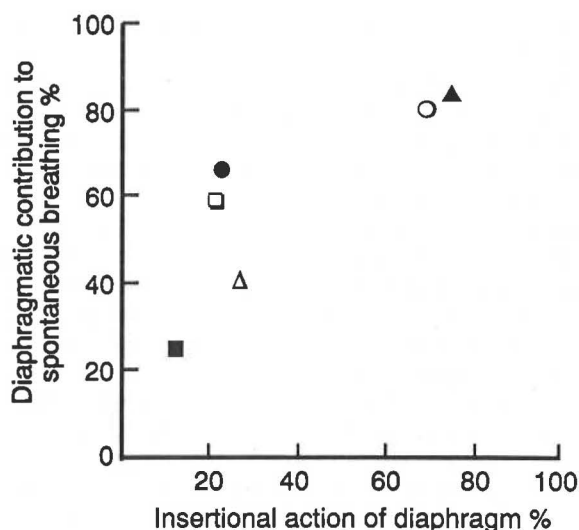


Fig. 9. - Relationship between the insertional component of diaphragm action and the diaphragm's contribution to the resultant displacement during spontaneous breathing ($r=0.84$, $p<0.001$).

These findings indicate that in spite of the large variability between dogs in the contributions of the various inspiratory muscle groups, supine anaesthetized dogs recruit whatever muscles are necessary so that rib cage and abdomen displacements are along or close to their relaxation characteristic.

Discussion

In applying vector analysis to the actions of the inspiratory muscles, we assume that displacement of the rib cage may occur independent of abdominal displacement and that PL may be altered independent of changes in Pab. In addition, the action of one muscle group on the chest wall must not influence the action of the second member of the vector pair. Others have also modelled the rib cage and abdomen as separate compartments and have considered the actions of the respiratory muscles as being independent of one another [2, 5-8] and evidence has been presented in humans showing that the degree of interdependence is small [9].

Our experiments were performed following upper abdominal surgery and the diaphragmatic contributions to displacement and pressure change may, therefore, have been underestimated because of reflex diaphragmatic inhibition [10, 11]. Since all dogs breathed close to their relaxation characteristic, however, this effect is likely to have been small.

Our analysis does not account for the contribution of the expiratory muscles to the inspiratory volume and pressure changes during spontaneous breathing. Under the conditions of this study (*i.e.* pentobarbital anaesthesia, no positive end-expiratory pressure and following laparotomy) abdominal muscle activity has been shown to be minimal [5]. Although no evidence of lowered end-expiratory rib cage position was apparent from the respiration signals and the oesophageal pressure tracings did not suggest expiratory muscle

contraction, these indices have been shown to be insensitive to triangularis sterni muscle activity [12]. Since passive recoil of the rib cage would have been associated with a negative (inward) influence on abdominal displacement, our analysis would have resulted in the inclusion of this contribution with that of the inspiratory rib cage muscles.

We used transvenous phrenic nerve stimulation to produce isolated diaphragmatic contraction. During spontaneous breathing the crural part generally contracts earlier and to a greater extent than the costal part [13]. Since phrenic stimulation activates all nerve fibres at the same frequency, at the same time, we may have underestimated the contribution of the crural part. Since this part displaces the rib cage and abdomen far from their relaxation characteristic, this would lead to underestimation of the RCM contribution to spontaneous breathing and tend to counterbalance any error introduced by reflex diaphragmatic inhibition.

The costal diaphragm acts to displace the rib cage through its anatomical insertions at the costal margins (insertional action) and by changing the pressure on the inner surface of the rib cage in the area of apposition. This pressure, averaged over the area of apposition, is closely related to P_{ab} [6, 14–16]. The crural diaphragm, which had no anatomical insertion on the rib cage, is considered to have an action which is entirely noninsertional. In the model presented by MACKLEM *et al.* [17] and ZOCCHI *et al.* [18], if the insertional component of the costal part were the only agency acting to displace the system, the same pressure would be applied to displace both the rib cage and abdomen and they would move along their relaxation characteristic. We therefore define "insertional" action as a displacement along the relaxation line and "noninsertional" action as that produced by crural contraction. This is similar to the concept of LORING and MEAD [6] who modelled the insertional component as a force applied to the rib cage at the costal margin by the diaphragm directed axially over and above the action of P_{ab} .

Our calculation of the insertional component of diaphragm action assumes that the appositional force is the same during costal and crural contraction. DECRAMER *et al.* [19] have demonstrated the distribution of abdominal pressures measured under the costal diaphragm, crural diaphragm, in the intestinal loops and in the stomach to differ under these conditions. This raises the possibility that inhomogeneity in the intra-abdominal pressure may have introduced an error into our estimate. Since it is likely that contraction of the crural part would result in a smaller change in subcostal pressure for a given mean intra-abdominal pressure change than would costal contraction, the effect of such an error would have been overestimation of the insertional component.

We did not attempt to partition the change in lung volume during spontaneous breathing. Theoretical models [17, 18] and the available experimental evidence [20] both indicate a parallel mechanical linkage between the insertional component of diaphragm action and the rib cage muscles. This means that when the insertional

component of diaphragm action is significant, partitioning of the volume change into the diaphragmatic and rib cage muscle contributions becomes impossible since they share the volume change. That is, when the diaphragm contracts the rib cage muscles shorten, either actively or passively. This is analogous to two pumps acting hydraulically in series. The output of one pump goes through the other. Both share the same output which is the total output of the system. If the insertional component is small it is possible to partition tidal volume approximately. It then becomes impossible, however, to partition the respiratory pressure swings as the algebraic sum of P_{di} and the pressure developed by the rib cage muscles, because under these conditions these two muscles act as two pumps hydraulically in parallel, therefore, the volumes displaced are additive but the pressures are not [17].

We found no significant difference between the diaphragmatic contribution to P_{ab} and to AB (fig. 8). This is to be expected because only P_{ab} acts to displace the abdomen and provides an internal check on the validity of our approach and data. The lack of equality between the diaphragmatic contribution to rib cage displacement and that to PL is also to be expected as PL is not the pressure driving the rib cage.

JIANG *et al.* [21] have also estimated the insertional action of the diaphragm. They found that with the respiband placed below the xiphoid process, isolated crural contraction inflated the lower rib cage along the relaxation relationship between rib cage displacement and P_{ab} . Costal contraction resulted in only slightly greater displacement for a given P_{ab} . They therefore concluded that the insertional action of the costal part was small in their dogs. What they refer to as "insertional" action, however, is different from our definition. They define it as the action of the costal diaphragm on the lower rib cage over and above that resulting from the change in P_{ab} . In spite of the difficulty in comparing their results with ours that this entails, and to the extent that we are likely to have overestimated the insertional component of P_{di} (see above), there would appear to be little difference in the results obtained except for the large between dog differences that we found.

They also showed that the mechanical coupling between upper and lower rib cage was rather loose. During rib cage distortions during phrenic stimulation the lower rib cage remained close to its relaxation characteristics, *i.e.* motion of the upper rib cage appeared to have little effect on the motion of the lower rib cage. Thus, in our experiments it is unlikely that the upper rib cage influenced the relationship between lower rib cage and abdominal displacement.

In the current study, the respitrace band was placed such that its mid-position was at the end of the xiphoid process and the remainder of the band lay within the zone of diaphragmatic apposition to the rib cage. This is somewhat higher than in the study of JIANG *et al.* [21] and lower than that of DE TROYER *et al.* [4]. In spite of these differences we confirmed that the actions of the costal and crural parts of the diaphragm differ.

However, their relative contributions to the action of the diaphragm and the contributions of the diaphragm and rib cage muscles to the displacements during spontaneous breathing were highly variable. This variability between dogs appears to be physiological rather than noise. Each dog was internally consistent. The standard error bars shown in figures 1-7 were similar for all dogs. We do not know the reasons for the physiological variability between dogs but suspect it lies in anatomical variability in body habitus. Despite this variability all animals breathed close to the relaxation characteristic. The inspiratory muscles appear to be recruited to preserve this relationship in spite of the large variability in individual muscle action. This accounts for the correlation between the diaphragmatic contribution to spontaneous breathing and the degree to which it displaces the rib cage and abdomen along their relaxation characteristic (fig. 9) and supports the previous suggestion that preservation of this breathing pattern may be important to the body's energy economy [22]. However, while it is now generally agreed that rib cage muscle recruitment is necessary in order to prevent distortions of the rib cage and abdomen away from the relaxation configuration, it has not previously been recognized that large variations between animals in the actions of the various respiratory muscle groups require marked differences between animals in the degree to which the rib cage muscles must be recruited in order to prevent distortions.

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