Deformation of the dog lung in the chest wall

SHAOBO LIU, SUSAN S. MARGULIES, AND THEODORE A. WILSON
Department of Aerospace Engineering and Mechanics, University of Minnesota, Minneapolis 55455; and Division of Thoracic Disease and Internal Medicine, Mayo Clinic, Rochester, Minnesota 55905

Liu, Shaobo, Susan S. Margulies, and Theodore A. Wilson. Deformation of the dog lung in the chest wall. J. Appl. Physiol. 68(5): 1979–1987, 1990.—Data on the shape of the chest wall at total lung capacity (TLC) and functional residual capacity (FRC) were used as boundary conditions in an analysis of the deformation of the dog lung. The lung was modeled as an elastic body, and the deformation of the lung from TLC to FRC caused by the change in chest wall shape and gravity were calculated. Parenchymal distortions, distributions of regional volume at FRC as a fraction of the volume at TLC, and distributions of surface pressure at FRC are reported. In the prone dog there are minor variations in fractional volume along the cephalocaudal axis. In transverse planes opposing deformations are caused by the change of shape of the transverse section and the gravitational force on the lung, and the resultant fractional volume and pleural pressure distributions are nearly uniform. In the supine dog, there is a small cephalocaudal gradient in fractional volume, with lower fractional volume caudally. In transverse sections the heart and abdomen extend farther dorsally at FRC, squeezing the lung beneath them. The gradients in fractional volume and pleural pressure caused by shape changes are in the same direction as the gradients caused by the direct gravitational force on the lung, and these two factors contribute about equally to the large resultant vertical gradients in fractional volume and pleural pressure. In the prone position the heart and upper abdomen rest on the rib cage. In the supine posture much of their weight is carried by the lung. This difference causes the difference between the distributions of regional volume in the prone and supine positions.

ventilation; pleural pressure; heart weight

THE DISTRIBUTION of ventilation in the human lung has been studied by measuring the dilution of test gases. It was indirectly measured by their concentration in expired gas and directly measured by the 23 emission of a radioactive gas within the lung. The ventilation distribution has been found to depend on posture, gravitational field, and the state of the muscles of the chest wall. These studies imply that the gravitational force on the lung and the shape imposed on the lung by the chest wall both affect the distribution of ventilation.

The distortion of the lung of the dog has been studied in more detail. Hoffman (3) reported distributions of the percent air content in the lungs of dogs, prone and supine, obtained from measurements of X-ray opacity by fast multislice computed tomography. A strong vertical gradient was found in the supine dog and a nearly uniform distribution was found in the prone dog. Ilbmayr et al. (4) and Rodarte et al. (11) measured the ventilation distribution and the distribution of strain that underlie the volume distribution with the use of radiopaque markers embedded in the parenchyma. They found a variability of ventilation in the prone dog but weak and variable spatial gradients of ventilation. The uniformly distributed variability of ventilation has been traced to a variability of parenchymal properties at small scale (10, 15). In the supine dog they found cephalocaudal and vertical gradients of ventilation. Their data describe the distortion of the parenchyma as well as the volume change. For example, they found that the lateral dimensions of an element of lung parenchyma in the upper lobe decreased by more than the dorsoventral or cephalocaudal dimensions as lung volume decreased. They reported magnitudes of the fractional length changes or strains in these three directions and spatial gradients of the three components of strain.

In one of the first mathematical analyses of lung deformation, West and Matthews (13) and Vawter et al. (12) computed the distortion of a body with an idealized upright human lung shape by the gravitational body force and by some idealized changes in chest wall shape. Subsequently, the mechanical properties of lung parenchyma that are needed to model the lung as a deformable body were measured (8), and lung deformations for simple local distortions and distortions of lobes under simple loading have been calculated (6). More recently, Bar-Yishay et al. (1) analyzed a model of the whole lung that included heart weight. The computed dependence of the vertical distribution of pleural pressure on heart weight was consistent with the measurements of esophageal pressure in upright dogs reported by Hyatt et al. (5).

The data on the shape of the chest wall of supine and prone dogs at total lung capacity (TLC) and functional residual capacity (FRC) reported by Margulies and Rodarte (9) provide the basis for more detailed modeling and analysis of the deformation of the lung in the chest wall. In this paper, we report the results of an analysis of the deformation of the lung caused by gravity and by the boundary displacements imposed on the lung by the chest wall.

METHODS

Data. The origin of the data on chest wall shape is described by Margulies and Rodarte (9). The displacement of the lung along the cephalocaudal axis was computed from the data on transverse area vs. axial position for all six dogs. The computed displacements for five of the six dogs were similar. Deformations in the transverse
planes were computed for two of the group of five dogs, and the results were similar. Computed deformations for one dog are reported.

**Analysis.** The deformation of the lung that accompanies the change in volume from TLC to FRC is divided into two parts. First, the lung is imagined to shrink isotropically from the volume at TLC (\(V_{\text{TLC}}\)) to the volume at FRC (\(V_{\text{FRC}}\)). Then the deformations that are caused by the change of boundary shape from the isotropically reduced lung shape to the observed shape at FRC and by the gravitational body force on the lung are computed. Local fractional volume at FRC, the ratio of the volume of an element of parenchyma at FRC to its volume at TLC, is the product of the uniform volume ratio \(V_{\text{FRC}}/V_{\text{TLC}}\) and the local volume ratio for the deformation of the isotropically reduced lung. Local pleural pressure is the sum of a uniform transpulmonary pressure at FRC and the pressure that accompanies the deformation.

To compute the deformation of the isotropically reduced lung caused by the change of shape and gravity, the lung is modeled as an elastic solid. Transpulmonary pressure at FRC is assumed to be 3 cmH\(_2\)O and values of the shear modulus \(\mu\) and bulk modulus \(k\) appropriate for this transpulmonary pressure are used: \(\mu = 2 \text{ cmH}_2\text{O}, k = 10 \text{ cmH}_2\text{O}\). The entire lung is modeled as a single body, and lobar fissures are not represented. It is assumed that the lung slides freely at the pleural surface and that the shear stress on this surface is zero.

Approximations are made in analyzing the deformation from the isotropically reduced lung to the shape at FRC. It is assumed that the shape of the transverse cross section of the isotropically reduced lung changes slowly along the cephalocaudal axis and that the difference between this shape and the true cross-sectional shape at FRC also varies slowly along the axis. If these conditions are met, plane transverse sections of the lung remain plane during the deformation, and the analysis can be considerably simplified. The set of equations that governs the deformation can be separated into two parts: one that governs displacements along the cephalocaudal axis and one that governs displacements in the transverse plane. The development that yields this decoupling is given in the appendix.

The conditions on which the simplifying approximations rest are fairly well satisfied. The quantity \(\frac{dA}{dz}\), where \(A\) is the cross-sectional area of the lung and \(z\) is the axial position, is a dimensionless measure of the rate of change of transverse dimension. Its magnitude is <0.3 over most of the axial extent of the lung. However, at the caudal and cephalad ends of the heart and at the dome of the diaphragm, the shape of the transverse section changes rapidly and the approximation is questionable at those points. We will focus on results obtained for transverse sections located within the midventral and middiaaphragm regions where the conditions are best met.

The data for transverse area vs. position along the cephalocaudal axis for the lung at TLC, the isotropically reduced lung, and the lung at FRC are shown in Fig. 1. The area vs. position for the isotropically reduced lung and the difference between this area and the area at FRC are the input data that appear in the equation that governs axial displacements, Eq. A9. The solution of this equation provides the mapping of the position of transverse planes from TLC to FRC. The transverse section of the thorax at TLC and at the location of this slice of parenchyma at FRC was chosen from the data. For each posture the two slices marked by arrows in Fig. 1 were analyzed. The shape of each slice at TLC, the isotropically reduced shape, and the shape at FRC are shown in Fig. 2. The finite element method was used to find the displacements in the transverse plane that are required to deform the plane section from the isotropically reduced shape to the shape at FRC. The density of the lung was assumed to be 0.3 g/cm\(^3\), and the gravitational body force on the lung was included in the analysis of the deformation in the plane.

**RESULTS**

The ratio of the thickness of a transverse lung slice at FRC to its thickness at TLC is plotted vs. its position at FRC in Fig. 3. If the lung shrank isotropically from TLC to FRC, the thickness ratio would equal the cube root of the volume ratio, 0.72. Regions in which the thickness ratio is >0.72 are stretched in the axial direction by the deformation from the isotropically reduced shape to the shape at FRC. The ratio of the area of a slice at FRC to its area at TLC is also shown in Fig. 3. If the lung shrank isotropically, the area ratio would equal the two-thirds power of the volume ratio, 0.52. Around the mediastinum the lung is stretched in the axial direction and compressed in transverse area, compared with an isotropic volume change. The distortions are in the opposite direction at the apex of the lung and between the heart and the dome of the diaphragm. The ratio of the volume of a slice at FRC to its volume at TLC shown in Fig. 3 is the product of the thickness and area ratios. The ratio of lung volume at FRC to lung volume at TLC is 0.37. The volume ratio of transverse slices is much more uniform than the thickness and area ratios. In the prone dog there is no overall trend of fractional volume with axial position. In the supine dog there is a slight trend, with fractional volume decreasing with distance from the apex.

Distributions of fractional volume over the transverse planes are described by level lines of equal fractional volume shown in Fig. 4. Fractional volume is fairly uniform over the transverse plane in the prone dog. Fractional volume passes through a minimum about midway between the ventral and dorsal regions, and local values of fractional volume differ from the mean by <10%. In the caudal section the lung is slightly compressed above the abdomen. The variation in fractional volume over the transverse planes is much bigger in the supine dog. The lung is compressed under the heart and abdomen and expanded in the horns that extend around the heart and abdomen.

The deformations in the transverse plane were also computed for the change in boundary shape, but without the gravitational body force. In dependent regions the horn of the lung of the prone dog and the dorsal region of the supine dog, fractional volume is smaller by ~0.03.
with gravity than without. In nondependent regions fractional volume is greater by 0.03.

The distortions of the parenchyma are illustrated in Fig. 5. The outlines of square samples of parenchyma in the lung at TLC are shown by dashed lines, and at FRC by solid lines. The distortions of the lung are less severe in the prone than in the supine posture. In the horns of the lung the parenchyma is compressed laterally and stretched in the dorsoventral direction. Near the sagittal midplane, the lung is compressed in the dorsoventral direction.

The pressure distributions on the pleural surfaces of the transverse slices are shown in Fig. 6. On the dorsal surface of the lung of the dog lying prone, pleural pressure is more negative than mean pleural pressure. Moving downward, pressure increases to about mean pleural pressure and is nearly uniform along the lateral surface. The calculated pressure near the ventral tip of the lung is quite negative, but the calculation is more sensitive to error in boundary data in this thin region. Pressure above the heart approximately equals mean pleural pressure. Pressure above the abdomen is more positive than mean pleural pressure. Moving downward along the lateral surface of the lung of the supine dog, pressure increases monotonically. The vertical gradient of pleural pressure is not constant. Its magnitude is $\sim 0.4$ cmH$_2$O/cm on the lateral surface of the caudal slice, smaller on the cephalad slice. Pressures below the heart and abdomen are 2-3 cmH$_2$O more positive than mean pleural pressure.

DISCUSSION

Some concerns about the modeling. It was assumed that the lung is uniformly expanded at TLC. Chevalier et al. (2) detected no difference between the shapes of dog lobes at TLC in situ and excised, presumably because at
TLC the lobes are stiff compared with the chest wall. We computed regional volume as a fraction of volume at 'TLC' by use of methods of linear elasticity. If the linear elasticity model is valid, the results are independent of the assumption that the lung is undeformed at TLC because the computed deformation can be superimposed on a preexisting deformation and the computed deformation describes the configuration of the lung at FRC relative to its configuration at TLC. The computed distribution of pleural pressure is the pressure distribution that accompanies the deformation from TLC to FRC. If there were preexisting strains at TLC, there would be additional stresses at FRC, and a more detailed argument is required to estimate the magnitude of this contribution to the pleural pressure distribution at FRC. Margulies and Rodarte (9) report that at TLC the location of the mediastinum and the shape of the diaphragm change with pneumothorax. These changes in chest wall shape with pneumothorax imply that with the lung intact at TLC, pleural pressure is not uniform. Nearly uniform lung expansion at TLC is compatible with nonuniform pleural pressure because the lung is stiff at TLC. The values of the elastic moduli, \( \mu \) and \( \kappa \), are large at TLC and the deformation that accompanies a given distribution of surface pressure is inversely proportional to the values of these moduli. Margulies and Rodarte (9) discuss the possibility of a gradient of pleural pressure of 1 cmH\(_2\)O/cm on the diaphragmatic surface of the lung at TLC. The small strains that accompany this gradient of pleural pressure at TLC are invariant to the isotropic volume change and would superimpose on the computed nonuniform deformation. The stresses at FRC are computed by use of values for the elastic moduli at FRC. Therefore, differences in pleural pressure at different points on the lung at TLC would transform to differences in pleural pressure at FRC that are smaller by the ratio of the values of the elastic moduli at FRC and TLC. The value of the shear modulus \( \mu \) increases linearly and the value of the bulk modulus \( \kappa \) increases more rapidly than linearly with transpulmonary pressure (8). Therefore, although there may be gradients in pleural pressure at FRC in addition to those we calculate, we expect the maximum gradient at TLC would be the gradient on the diaphragmatic surface and that this gradient transforms to a gradient of about \( \leq 0.1 \) cmH\(_2\)O/cm at FRC.

Lobar fissures were not represented in the model. Relative displacements and rotations of lobes that are allowed by sliding at lobar fissures provide an additional mechanism for adjusting the shape of the lung to the shape of the chest wall. We would expect that smaller deformations of the parenchyma would be predicted if lobar fissures were represented in the model. There were transverse slices for which the area within the rib cage was filled with lung at TLC, but partly filled by heart or abdomen at FRC. The drastic changes in shape of the boundary of the lung in these slices must be accommodated by relative rotations and displacements of the lobes. Also, attachments to the lobar bronchi were not represented in the model. Forces transmitted to the parenchyma through the bronchi would cause additional strains and stresses that would be largest at the points where the bronchi enter the parenchyma and decrease rapidly with distance from those points (7).

A general property of the computed deformation. The \( \mu \) describes the stiffness of a material for changes of shape and the \( \kappa \) describes the stiffness for changes of volume. The \( \mu \) of lung parenchyma is small compared with its \( \kappa \), and parenchyma changes shape more easily than it changes volume. The computed deformations show this property. The maximum axial and transverse area strains in the deformation from the isotropically reduced volume to FRC are \( \sim 0.2 \). However, the axial strains and transverse area strains shown in Fig. 3 are opposed. At points where the material is stretched axially, it is compressed in the transverse plane and vice versa. As a result, volume differs from the mean by \( < 10\% \). The same pattern of compensatory strains appears in the deformations in the transverse plane shown in Fig. 5. Compression in one direction accompanies extension in the perpendicular direction, and the shear strains are larger than the volume strains.
Comparison between the computed deformation and data from computed tomography and parenchymal markers. In Fig. 3 local variations in fractional volume are shown near the cephalad end of the heart and near the dome of the diaphragm. In the prone dog there is no mean axial gradient of fractional volume. In the supine dog there is an overall cephalocaudal trend in fractional volume with an average slope of about -0.01/cm.

Hubmayr et al. (4) measured the volumes enclosed within tetrahedra formed by radiopaque markers embedded in the parenchyma. They found no cephalocaudal gradients of fractional volume in the prone dog. In the supine dog they found that the fractional volume of the caudal lobe was smaller than that of the cephalad lobe, and they found cephalocaudal gradients in both lobes. The axial gradients in the lobes were between -0.01 and -0.02/cm. The direction of the gradient predicted by the deformation analysis is the same as the direction of the observed gradients, and the magnitude of the local slopes at the cephalad end of the heart and the dome of the diaphragm is about the same as the observed slope, but the overall slope of the computed fractional volume distribution is smaller than the observed slope.

The axial extension ratios and transverse area ratios that underlie the axial distributions of fractional volume are also shown in Fig. 3. These show stronger variations...
along the axis than the distribution of fractional volume. In general the lung around the heart is compressed in the transverse plane and stretched axially from the isotropically reduced shape. Near the dome of the diaphragm the transverse and axial distortions are reversed. Rodarte et al. (11) report the fractional decrease in parenchymal dimensions in the axial and the two transverse directions for upper and lower lobes of prone and supine dogs. The lobes overlap along the z axis, but some agreement can be found between the computed deformation around the heart and their data for the upper lobe and between computed deformation near the top of the diaphragm and their data for the lower lobe. They report that the decrease between TLC and FRC of the axial dimension of the upper lobes of both prone and supine dogs is less than the mean decrease of the transverse dimensions. The relative magnitudes of the decrease in axial and transverse dimensions are reversed in the lower lobes of the supine dogs. No consistent pattern was found in the lower lobes of prone dogs.

The fractional volume distributions in the transverse planes shown in Fig. 4 are quite different for the prone and supine positions. Fractional volume is nearly uniform in the transverse plane of the prone dog. Without gravity, a reverse gradient is predicted with smaller fractional volumes in the nondependent dorsal region than in the anterior dependent region. The gradient of fractional volume caused by the gravitational body force is in the opposite direction from the gradient caused by the change in boundary shape, and the result is a relatively uniform distribution with a minimum fractional volume midway in the vertical extent of the lung. Hoffman (3) measured the local radiopacity of the lungs in prone and supine dogs. He found a very slight reverse gradient of fractional volume in the prone posture. Hubmayr et al. (4) found no consistent vertical gradient of fractional volume in the prone dog.

Strong variations of fractional volume in the transverse sections of the supine dog are computed. The gradients produced by the change in boundary shape are in the same anatomical direction as for the prone dog but much larger because the heart and abdomen extend farther dorsally at FRC in the supine dog. In the supine posture the gravitational gradient adds to the gradient produced by the boundary shape change. About 60% of
DEFORMATION OF THE DOG LUNG

1985

PRONE

SUPINE

FIG. 6. Pressure distributions at pleural surface of transverse slices.

The distortions that underlie the fractional volume distributions in transverse planes are illustrated in Fig. 5. The distortions are small in the cephalad transverse section of the prone dog. In the caudal section parenchyma in the ventral horn is compressed laterally and extended in the dorsoventral direction. In the dorsal region near the midplane the directions of compression and extension are reversed. In the supine dog the anatomic pattern is the same as in the caudal section of the prone dog, but the distortion is more extreme. Rodarte et al. (11) reported the fractional changes in the dimensions of parenchyma between TLC and FRC. They found that the lateral dimension changed by more than the anteroposterior dimension. The computed deformation in lateral regions of the lung is consistent with these data. Rodarte et al. (11) also reported gradients of the strain components. These were quite variable among the dogs. The strongest and most consistent gradient was the dorsoventral gradient in the dorsoventral strain in the supine dog. The dorsoventral dimension decreased more dorsally than ventrally. This is consistent with the deformations shown in Fig. 5.

Pressure distributions and the support of the weight of the heart and abdomen. The pressure distributions shown in Fig. 6 are similar to the fractional volume distributions. In the prone position pleural pressure is more negative at the dorsal and ventral ends of the lateral surface and there is a minimum in the magnitude of pleural pressure along the lateral surface. Wiener-Kronish et al. (14) found a vertical gradient in pleural pressure of \(-0.25\) cmH\textsubscript{2}O/cm on the lateral surface of prone dogs. In the supine position, pleural pressure increases moving downward along the lateral surface. The gradient is larger at the ventral end of the lateral surface but roughly agrees with the value 0.4-0.5 cmH\textsubscript{2}O/cm reported by Wiener-Kronish et al. (14) for supine dogs.

Pressure above the heart of the prone dog is approximately mean pleural pressure. Pressure above the abdomen is somewhat higher. Margulies and Rodarte (9) note that the dorsoventral dimension of the lower rib cage was smaller in the prone than the supine posture. The sling that supported the prone animal may have raised the abdomen above its physiological position. The vertical extents of the heart and abdomen in the sections that are pictured are \(-6\) cm. A pressure difference between the top and bottom of the heart and abdomen equal to their vertical extent is required if the slices of heart and abdomen are supported by the pressures that act on their boundary. By this argument the pressure at the surfaces where the heart and abdomen rest on the rib cage of the prone dog is estimated to be \(-3\) cmH\textsubscript{2}O, 6 cmH\textsubscript{2}O more positive than mean pleural pressure. In the supine dog the pressure beneath the heart and abdomen is 3 cmH\textsubscript{2}O more positive than mean pleural pressure, and the pressure at the surface of the rib cage above the heart and abdomen is estimated to be 3 cmH\textsubscript{2}O more negative than mean pleural pressure, about \(-6\) cmH\textsubscript{2}O.

In the prone dog the pressure at the surface of the lung above the heart and abdomen is not distorted by the weight of the heart and abdomen below the lung. The heart and abdomen can be said to rest on the rib cage. In the supine dog the weight of the heart and abdomen

The vertical gradient of fractional volume in the supine dog is not uniform over the vertical extent of the lung. It is stronger in the ventral horn than in the dorsal region. A value of 0.02/cm roughly describes the magnitude of the gradient of fractional volume in the bulk of the lung. Hoffman (3) reports clear vertical gradients in percentage of air content in supine dogs. The gradients are consistent among dogs and develop regularly with decreasing lung volume. The magnitude of the gradient at FRC is \(-3\)% air content/cm. The gradient of percent air content implies a gradient of fractional volume that is opposite in sign and at FRC approximately equal in magnitude to the gradient in percent air content. Hubmayr et al. (4) report a gradient of fractional volume of \(-0.03 \pm 0.01/cm\) in six upper lobes and four lower lobes of supine dogs. The predicted gradients are somewhat smaller than the observed gradients. Perhaps the values of transpulmonary pressure and bulk modulus that were used in the computation are somewhat higher than the true values at FRC. Also, the values of the bulk modulus that were used in the analysis describe the slope of a pressure-volume loop; the bulk modulus that describes the slope of the deflation limb is smaller.

The total gradient is a result of the distortion by the change of boundary shape and 40% is contributed by the gravitational force on the lung.

Margulies and Rodarte report that the dorsoventral dimension of the lower rib cage was smaller in the prone than the supine posture. The sling that supported the prone animal may have raised the abdomen above its physiological position. The vertical extents of the heart and abdomen in the sections that are pictured are \(-6\) cm. A pressure difference between the top and bottom of the heart and abdomen equal to their vertical extent is required if the slices of heart and abdomen are supported by the pressures that act on their boundary. By this argument the pressure at the surfaces where the heart and abdomen rest on the rib cage of the prone dog is estimated to be \(-3\) cmH\textsubscript{2}O, 6 cmH\textsubscript{2}O more positive than mean pleural pressure. In the supine dog the pressure beneath the heart and abdomen is 3 cmH\textsubscript{2}O more positive than mean pleural pressure, and the pressure at the surface of the rib cage above the heart and abdomen is estimated to be 3 cmH\textsubscript{2}O more negative than mean pleural pressure, about \(-6\) cmH\textsubscript{2}O.


Pressure above the heart of the prone dog is approximately mean pleural pressure. Pressure above the abdomen is somewhat higher. Margulies and Rodarte (9) note that the dorsoventral dimension of the lower rib cage was smaller in the prone than the supine posture. The sling that supported the prone animal may have raised the abdomen above its physiological position. The vertical extents of the heart and abdomen in the sections that are pictured are \(-6\) cm. A pressure difference between the top and bottom of the heart and abdomen equal to their vertical extent is required if the slices of heart and abdomen are supported by the pressures that act on their boundary. By this argument the pressure at the surfaces where the heart and abdomen rest on the rib cage of the prone dog is estimated to be \(-3\) cmH\textsubscript{2}O, 6 cmH\textsubscript{2}O more positive than mean pleural pressure. In the supine dog the pressure beneath the heart and abdomen is 3 cmH\textsubscript{2}O more positive than mean pleural pressure, and the pressure at the surface of the rib cage above the heart and abdomen is estimated to be 3 cmH\textsubscript{2}O more negative than mean pleural pressure, about \(-6\) cmH\textsubscript{2}O.
is carried by both the lung and the rib cage. The heart and abdomen move downward to a position at which the pressure beneath them is increased by 3 cmH₂O and the pressure above them is decreased by 3 cmH₂O. Half their weight is transmitted down through the lung and half around and down through the structure of the rib cage. Margulies and Rodarte (9) report that in the supine dog the heart is located more dorsally at FRC than at TLC, and that if falls further with pneumothorax. The inference drawn from the analysis of lung deformation about the support of the heart are consistent with these observations.

**Summary.** The agreement between the properties of the computed deformation of the lung and data on fractional volume distributions, strains, and pleural pressure distributions imply that the model describes the response of the lung to change of chest wall shape and gravity. The major features of the deformation follow from the features of the shape change. Margulies and Rodarte (9) show that between TLC and FRC the transverse area enclosed by the rib cage changes by a constant fraction over its cephalocaudal extent, but the volume of the mediastinum increases slightly. As a result, the transverse area available to the lung decreases nonuniformly, and the lung is squeezed around the mediastinum. Compression of an elastic material in one direction promotes extension in a perpendicular direction, and the lung extends axially where it is compressed transversely.

In transverse planes there are mismatches between the TLC boundary shape, isotropically reduced, and the shape at FRC. In the prone dog the ventral tips of the lung are bent outward and stretched ventrally. There is some dorsoventral compression above the heart and abdomen. The compression above the abdomen may be accentuated by the sling support. The shape change produces slight reverse gradients in fractional volume and pleural pressure that oppose the gradients produced by gravity. In the supine dog the change of shape of the transverse section is more severe. There is the same bending and ventral stretching of the ventral horns of the lung, and there is a lateral compression of the horns. The major difference between the shape changes for the prone and supine positions is the large dorsoventral compression under the heart and abdomen in the supine position. The weight of the heart and abdomen compresses the lung beneath them, and the effects of shape change and gravity add to produce strong vertical gradients of fractional volume and pleural pressure.

**APPENDIX**

The equilibrium state of an elastic solid is the state, compatible with the boundary conditions, for which the elastic energy of deformation is minimum. The total elastic energy $E$ is the integral of the energy per unit volume $e$ over the volume $V$

$$e = \frac{1}{2} \left[ (\lambda + 2\mu) (\epsilon_x^2 + \epsilon_y^2 + \epsilon_z^2) + 2\lambda (\epsilon_{xy} + \epsilon_{xz} + \epsilon_{yz}) \right] + \mu (\epsilon_x^2 + \epsilon_y^2 + \epsilon_z^2)$$  \hspace{1cm} (A1)

In Eq. A1, $\lambda$ and $\mu$ are the Lamé constants that describe the elastic properties or stiffness of the solid; $\epsilon_x$, $\epsilon_y$, and $\epsilon_z$ are the normal components of strain; and $\epsilon_{xy}$, $\epsilon_{xz}$, and $\epsilon_{yz}$ are the shear strains. A coordinate system is chosen in which the $x$ axis lies in the cephalocaudal direction and the $x$- and $y$-axes lie in transverse planes. The displacements in the $x$, $y$, and $z$ directions are denoted $u_x$, $u_y$, and $u_z$, respectively. The relationships between the strains and the displacements are given by the following equations

$$\epsilon_x = \frac{\partial u}{\partial x} \quad \epsilon_y = \frac{\partial v}{\partial y} \quad \epsilon_z = \frac{\partial w}{\partial z}$$

$$\epsilon_{xy} = \frac{\partial u}{\partial y} + \frac{\partial v}{\partial x} \quad \epsilon_{xz} = \frac{\partial u}{\partial z} + \frac{\partial w}{\partial x} \quad \epsilon_{yz} = \frac{\partial v}{\partial z} + \frac{\partial w}{\partial y}$$  \hspace{1cm} (A2)

By substituting these expressions for the strains into Eq. A1, the integral to be minimized

$$E = \int e \ dx \ dy \ dz$$  \hspace{1cm} (A3)

is expressed as a functional of the three functions, $u$, $v$, and $w$.

It is assumed that the transverse cross sectional area of the lung $A(z)$ and the strains vary slowly with $z$ and that transverse planes in the lung remain plane as the lung deforms. Consistent with these assumptions about the geometry of the body and the deformation, it is assumed that the shear strains, $\epsilon_{xy}$ and $\epsilon_{xz}$, are negligible, that the transverse displacements $u$ and $v$ vary with $x$ and $y$ and more slowly with $z$, and that $w$ is a function of $z$ only.

The simplifying assumptions about the nature of the deformation lead to a decoupling of the equations governing the axial displacement $w$ and the equations governing the transverse displacements $u$ and $v$. The transverse displacements and normal strains are written in the form

$$u = \bar{u} + u' \quad \epsilon_x = \bar{\epsilon} + \epsilon'$$

$$v = \bar{v} + v' \quad \epsilon_y = \bar{\epsilon} + \epsilon'$$  \hspace{1cm} (A4)

where $\bar{\epsilon}$ is the average normal strain in the transverse plane and $u'$ and $v'$ are local differences from the displacements that correspond to the average strains

$$\int (\epsilon_x + \epsilon_y) dx dy = 2\Lambda A$$

$$\int \epsilon_x dx dy = \int \epsilon_y dx dy = 0$$  \hspace{1cm} (A5)

The integral of the sum of the normal strains has a geometric interpretation; it is the area change of the slice.

With these expressions for the transverse strains substituted into Eq. A1, the integral over the transverse plane reduces to the following expression

$$\int e \ dx \ dy = F + G$$

$$F = (A/2)[((\lambda + 2\mu)(\bar{\epsilon}^2 + \bar{\epsilon}^2) + 2\lambda (\bar{\epsilon}_x \bar{\epsilon}_x + \bar{\epsilon}_y \bar{\epsilon}_y + \bar{\epsilon}_z \bar{\epsilon}_z)]$$

$$G = \frac{\mu}{2} \int (((\lambda + 2\mu)(\epsilon'_x + \epsilon'_y) + 2\lambda \epsilon'_x \epsilon'_y + \mu \epsilon'_z) dx dy$$  \hspace{1cm} (A6)

The terms outside the integral on the right side of Eq. A6, denoted $F$, are functions of $z$ only.

In the analysis of the nonuniform part of the deformation from TLC to FRC, the isotropically reduced lung shape is taken as the undeformed shape of the lung. $A(z)$ denotes the transverse area as a function of axial position of the isotropically shrunken lung, shown by the dashed line in Fig. 1. At such $z$, the area of the deformed shape, shown by the solid line in Fig. 1, differs from the area of the undeformed shape by an amount $\Delta A$. In addition to the area change $\Delta A$, the area of each slice changes because it is displaced to a position where the undeformed area is different. The area change of each slice equals the sum of the area difference at its original position and the
DEFORMATION OF THE DOG LUNG

2\Delta A = \Delta A + w(d\Delta A/dz) \quad (A7)

Equation A7 provides an expression for \( \epsilon \) in terms of the known functions of \( \epsilon, \Delta \Delta A \) and \( d\Delta A/dz \), and the unknown function \( w \). Substituting this expression for \( \epsilon \) yields the following expression for \( F \)

\[
F = \frac{1}{2}\epsilon([\lambda + \mu](\Delta A + w(d\Delta A/dz))^2/A + 2\lambda(\Delta A + w(d\Delta A/dz))k_\epsilon + (\lambda + 2\mu)A\epsilon_\phi^2)
\]

(A8)

The unknown function \( w \) and its derivative \( \epsilon \) appear in \( F \) but not in \( G \). Therefore, minimizing \( \int F \) with respect to \( w \) is equivalent to minimizing the strain energy with respect to \( w \). The Euler equation that results from setting the variation of \( \int F \) with respect to \( w \) equal to zero is the following

\[
A(\lambda + 2\mu)(dA(dw/dz)/dz) - (\lambda + \mu)(dA/dz)^2)w + \Lambda A(d\Delta A/dz) - (\lambda + \mu)\Delta A(dA/dz) = 0
\]

(A9)

The unknown functions \( u \) and \( v \) appear only in \( G \). \( G \) is the strain energy for plane strain. Therefore, the problem of the deformation in the transverse plane is the standard problem of plane strain with given normal displacements at the boundary.

The normal displacement was set equal to the normal distance between the isotropically reduced shape of the slice and the shape of the slice at its location at FRC. The tangential displacement was unspecified to represent the absence of shear stress at the surface. Standard finite element methods were used to obtain the displacements and area ratios in the plane. The normal stress at the boundary was obtained and a uniform normal stress of 3 cmH2O was added to obtain the pleural pressure distribution shown in Fig. 6.

This study was supported by National Heart, Lung, and Blood Institute Grants HL 21584 and HL 4684.

Address for reprint requests: T. A. Wilson, 107 Akerman Hall, University of Minnesota, Minneapolis, MN 55455.

Received 17 January 1989; accepted in final form 21 December 1989.

REFERENCES