J. Physiol. (1977), 266, *pp.* 499–521
With 14 *text-figures*
Printed in Great Britain

THE CHANGES IN CONFIGURATION OF THE RIB CAGE AND ABDOMEN DURING BREATHING IN THE ANAESTHETIZED CAT

BY K. M. C. DA SILVA,* B. McA. SAYERS, T. A. SEARS AND D. T. STAGG

From the Department of Electrical Engineering Applied to Medicine, Imperial College of Science and Technology, London and from the Sobell Department of Neurophysiology, Institute of Neurology, Queen Square, London WC1N 3BG

(*Received 11 October 1976*)

SUMMARY

1. The external surface of the rib cage and abdominal wall in anaesthetized cats was surgically exposed in order to record their movements cinematographically in spontaneous breathing and in paralysed cats, during artificial positive pressure ventilation.

2. Cine-stereophotography was used to allow the recording of the movements of a set of markers placed on the external surface of the trunk wall and the corresponding stereometric data were numerically and graphically processed into three-dimensional drawings. The cine-film frames corresponding to the phases of maximum inflation and deflation of the lungs were analysed to reveal the changes in configuration associated with the respiratory movements of the trunk wall.

3. The changes in shape of the diaphragm and the displacements of the abdominal viscera between extreme inflation and deflation were recorded by X-ray photography.

4. During spontaneous inspiratory movements, the ribs rotated outwards and rostrally about the costovertebral joints bringing about an increase in the transverse dimensions of the cage all along its length; these movements were accompanied by a clear-cut caudad displacement of the sternum, caused by the straightening of the costal cartilages and by the widening of the angles defined at sternochondral joints between the sternum and each of the costal cartilages.

5. Neuromuscular blockade abolished muscle tone in the trunk wall, allowing the weight of the viscera markedly to deform its configuration.

---

* Present address: Centro de Biologia, Fundacao Calouste, Gulbenkian, Lisbon, Portugal.

6. The inspiratory rib movements of the paralysed animal during artificial inspiration were similar to those during spontaneous breathing but the movements of the sternum were inverted and showed small cranial displacements.

7. The loss of muscular tone under neuromuscular blockade made the abdominal wall more compliant than the rib cage to the positive lung pressure and allowed greater mobility of the viscera with consequent distortion of the shape of the diaphragm.

8. The role of rib cage muscle tone in meeting requirements of purely configurational character in such a shell-like structure is discussed in relation to the optimal mechanical performance of the diaphragm.

INTRODUCTION

During the last decade, there has been a shift of emphasis in respiratory mechanics from the use of the 'relaxation pressure curve' of the lungs and thorax, as used by Rahn, Otis, Chadwick & Fenn (1946) to the more specific analysis of the separate pressure volume curves of the rib cage and abdomen described by Konno & Mead (1967, 1968). For example, in this latter study, based on the analysis of the separate motions of the rib cage and abdomen, it was shown that previous estimates of the work of breathing, which had included the work done on the chest wall, were based on the incorrect assumption that the configuration of the chest wall during breathing is the same as that which occurs during voluntary relaxation against a closed airway at the same lung volume; Konno & Meads' measurements showed this not to be the case.

In man, the rib cage accounts for 66 % of the vital capacity in the supine posture and in the upright 70 % (Konno & Mead, 1967). As a thin-walled shell-like structure the rib cage has to withstand the fall in transthoracic pressure produced by the action of the diaphragm. Also, as the rib cage itself expands through the action of the intercostal muscles to increase lung volume, it must resist internal stresses as well as those arising externally due to the action of muscles which connect with the rib cage. Changes in rib cage configuration must be of particular importance for the efficient operation of the rib cage, quite apart from the implication such changes in shape also have for the optimal performance of the diaphragm (Marshall, 1962; Pengelly, Alderson & Milic-Emili, 1971).

Unfortunately, there has been no similar analysis of these shape changes in the cat, the animal about which most is known neurophysiologically. Without one, no deep understanding is possible of the relevant mechanical properties of the respiratory system nor of the design features of the nervous mechanism which controls it, particularly with regard to servo control of the intercostal muscles (Sears, 1973; Euler, 1973). In this paper we describe how, for the anaesthetized cat, we have used stereophotography combined with X-ray photography to provide a description in three dimensions of the movements of the rib cage, diaphragm and abdominal wall during spontaneous breathing and compared them with those which occur under artificial ventilation in the paralysed animal.

METHODS

Principle of the method. The changes in the shape of the trunk wall surface during breathing were recorded by stereo-cinephotography. This was achieved by using a system of mirrors (Fig. 1) to obtain simultaneous views of the dorsal, ventral and lateral surfaces of the body on single frames of a cine-film. A set of small markers was glued to the chest and abdominal wall surfaces after the skin had been removed, each marker defining a point on the surface whose position with respect to a fixed frame of reference, the base plate of the mirror system, could be computed. In this initial kinematic study of the breathing movements we were particularly interested in defining the motions of the ribs and abdominal wall surfaces and to achieve this we had to apply the markers directly to them. A number of conveniently chosen film frames were magnified and in each frame the planar co-ordinates of the stereo-image pairs of the markers were read and then processed on a digital computer to yield, for each marker in the frame, the three co-ordinates which specify its position in space. Finally, using this set of marker points as a framework together with some additional data measured on the animal, the ribs and the trunk wall surface were drawn as three-dimensional bodies for each of the film frames studied. The accuracy of the method was assessed by applying the analytical procedure to the cine-photographs of a test cylinder (Appendix).

Preparation of the animal. The experiments were performed on four cats anaesthetized with pentobarbitone sodium (40 mg/kg, supplemented as required), tracheostomized and connected to a calibrated recording spirometer. The actual film sequences were completed within a few minutes so that changing levels of anaesthesia were not a problem. The animal was paralysed when required by gallamine triethiodide (Flaxedil) and artificially ventilated under positive pressure from a Palmer–Ideal pump. As shown in Fig. 1, the animal was rigidly supported in the prone position in a Canberra-style animal frame by means of clamps placed on the vertebral spines at T1, T11 and on the iliac crests. In this way the chest and abdomen were pendant. The vertebral column was positioned horizontally and considerable care was taken to ensure that it was straight and that the sagittal plane of the body was parallel to the base plate of the mirror system. When positioned correctly the images on the mirrors showed complete views of the dorsal and ventral surfaces of the animal's body. A skin flap was formed to allow exposure of the entire area to be delineated by the markers. All the superficial muscles overlying the thoracic wall, such as the latissimus dorsi, serratus and pectoral muscles were removed to expose the ribs and the intercostal, rectus and abdominal oblique muscles. These exposed surfaces were covered by the skin flap as much as possible during the dissection and kept continually moistened with 0·9 % saline. The dorsal extensor muscles were left intact to preserve the structural integrity of the vertebral column.

Application of markers. Preliminary experience showed that it was better to film in colour and to use coloured reflective markers. The markers were formed from a short length of PVC sleeving whose lateral and end surfaces were covered by red

Scotchlite tape (Minnesota Mining and Manufacturing Co. Ltd); the over-all dimensions of each marker were a length and diameter of 2·5 mm. The markers were stuck to the body with surgical glue (DUO, Johnson & Johnson) and positioned to outline the ribs, costal cartilages and the surface of the abdomen. The use of a highly reflective marker and spotlight illumination gave a good contrast against the shining wet muscle surface. The size of the marker was optimized for obtaining a good image of it on the curved surface of the body as viewed directly or through the mirrors. At the end of each experiment detailed notes were made of the position of markers with respect to the ribs and other salient structural features. The animal was killed and the thorax preserved for subsequent measurement of the lengths of all the ribs.

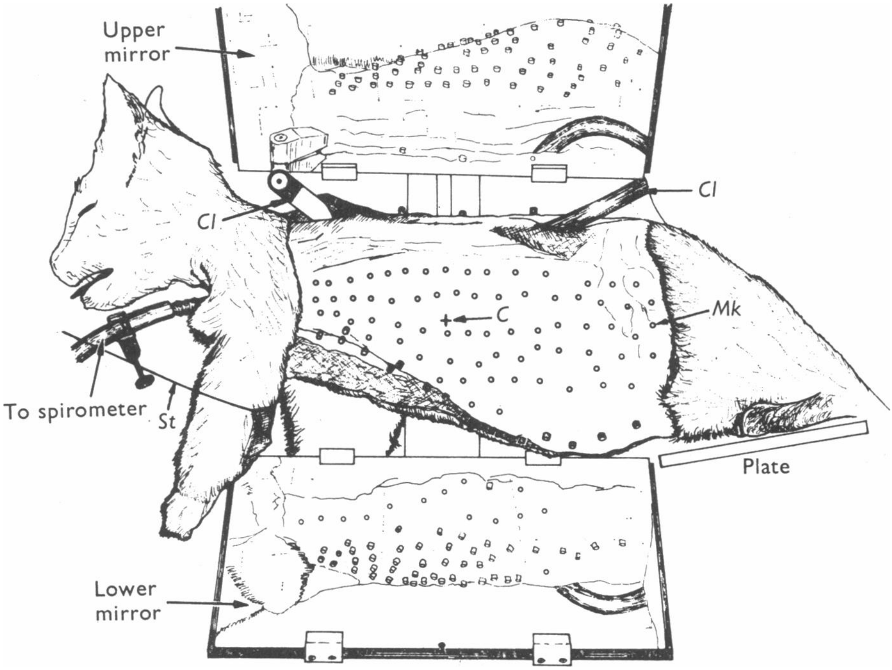

Fig. 1. Experimental set-up. The animal is held in position by two spinal clamps (*Cl*), his hind limbs rest on a metal plate, his head is supported by a string and the skin flap is kept out of the way by another string (*St*). The reflective markers (*Mk*) are glued to ventral and lateral surfaces of the trunk and to the spine and each one is visible directly and at least on one of the mirrors. The location of the optical centre (*C*) on the photograph is indicated by a cross.

Photographic system. Stereo records were obtained by means of the mirror system shown diagrammatically in Fig. 2 and consisting of a supporting base and two plane mirrors whose reflecting surfaces were orientated at 30° with respect to the plane of the base. When in use the base was firmly mounted on the Canberra-type frame and had its main axis orientated vertically. All metallic parts in this structure were in duraluminium and machined to an accuracy of $\pm 25\ \mu$m; the angle of the mirror surfaces relative to the base was defined to within half a minute of arc. The plane mirrors were 3 × 160 × 280 mm glass plates whose ground polished and front aluminized surface was flat to less than ten mercury line wave-lengths as measured in a Fizeau interferometer. The brackets on which the mirrors were mounted could be moved sideways along the base of the system in order to optimize the reflected images of the animal surface; the accuracy of the position of the mirrors relative to the base was guaranteed by a longitudinal slot in which the base of the brackets fitted tightly. Fig. 2 also shows the light pencil (*LP*) which was used for the alignment of the camera in a direction perpendicular to the base of the mirror system. This device consisted of an accurately machined rod, 280 mm long, arising from a broad cylindrical base by which it was mounted on the base of the system. The rod was machined to create a longitudinal bore of 0·6 mm effective diameter through which could be seen the light of a torch bulb located inside the cylindrical base. The camera was aligned by *zooming* on the light pencil until its image filled the entire photographic field and then moving the camera on its tripod until the light at the base of the light pencil was seen at its maximum brightness. In this way the optical axis of the camera could be brought to coincide with the optical axis of the system of mirrors with an angular error calculated to be less than fifteen minutes of an arc; this error was neglected in our computations.

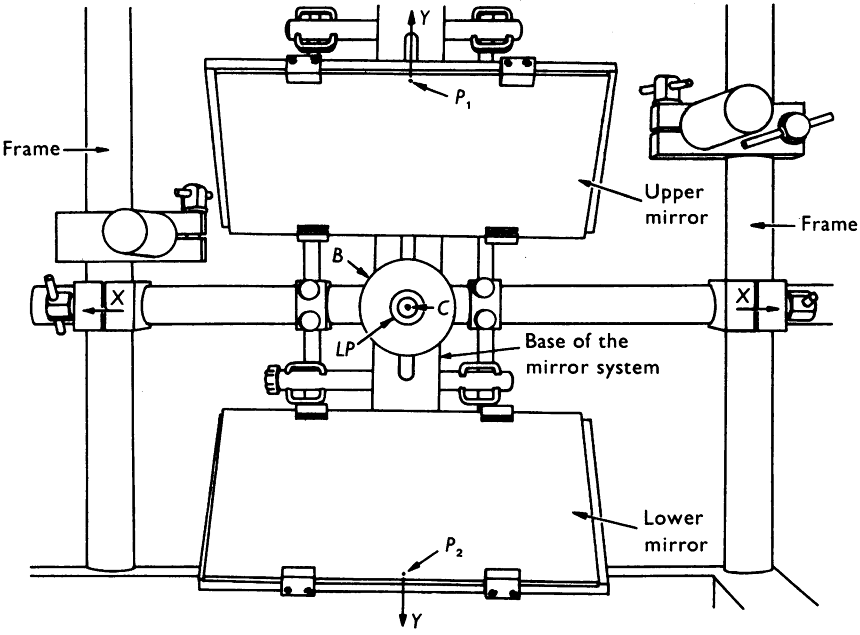

Fig. 2. Tracing of a photograph showing the mirror system mounted on the Canberra-style frame. The mirrors are fixed in position along their common base which is clamped vertically to the frame; two markers (P_1 and P_2) are glued to the mirrors to define the vertical YY-axis. Also shown is the frontal view of the light pencil (*LP*), its base (*B*) and the optical centre (*C*) which the centre of the pencil defines. The horizontal XX-axis of the photograph is the perpendicular to the YY-axis which passes through *C*.

Photography. The photographic recording was made with an Arriflex 16-mm cine-camera, equipped with a zoom lens (Som Berthiot 1/3.8). An Ektachrome EF 7242 Kodak colour film was used and the preparation was illuminated with a 500 W spotlight placed immediately underneath the camera and aligned with its optical axis. The camera was located at 285 cm from the base of the mirror system and the lens adjusted for a focal distance of 60 mm with the aperture set at 4·5; the filming speed was sixteen frames per second. At the beginning of each experiment the camera was aligned and held in exactly the same position throughout the experiment. The first sequence filmed recorded the mirror system and the light pencil in order to establish the optical centre (C) of the system. Circular markers (P_1 and P_2) were placed on the external edge of each mirror, at points indicated on the mirror bases which were aligned with the axis of symmetry of the entire mirror system; these two markers were thus co-linear with the centre (C) of the light pencil and the three points defined the vertical YY-axis of the photograph for all film frames. After it was photographed, the pencil was removed and the calibration cylinder (Appendix) bearing a set of markers was mounted on the animal frame and filmed.

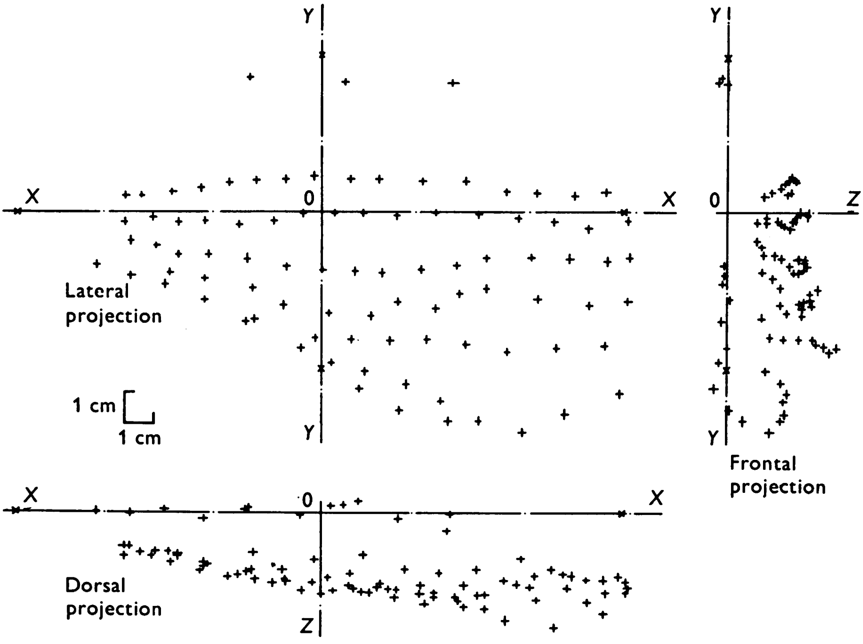

Fig. 3. Three orthogonal XY (lateral), XZ (dorsal) and YZ (frontal) projections of the set of marker points in one cine-frame obtained after processing the corresponding stereometric data. The XX- and YY-axes are those defined on the plane of the photograph and the ZZ-axis represents depth measured from the median plane of the body.

X-ray photography. Dorsal and lateral views of the animal were taken using a mobile camera. The system of mirrors could easily be removed so that the vertical cassette for the lateral view could be placed immediately behind the animal.

Analysis of the records. The calculations described below were done on an IBM 1800 computer. A set of film frames was selected for analysis together with the relevant frames of the calibration procedure obtained at the beginning of the experiment. Typically the set comprised every third frame over a period of four or five respiratory cycles. The picture in each frame was projected on a ground-glass plate as an image magnified to twice the real size and the positions of the markers on it, as seen in the direct and mirror views, were transferred to a sheet of plastic tracing paper; the calibration markers which located the ordinate and optical axes were also transferred. Next the tracing was placed on an XY-digitizer (Mark I pencil follower, D-mac Ltd, London) and the co-ordinates of the axes and the markers were read and punched on to computer cards. A computer program used the formulae given in the Appendix to compute the XY and Z orthogonal co-ordinates for each marker.

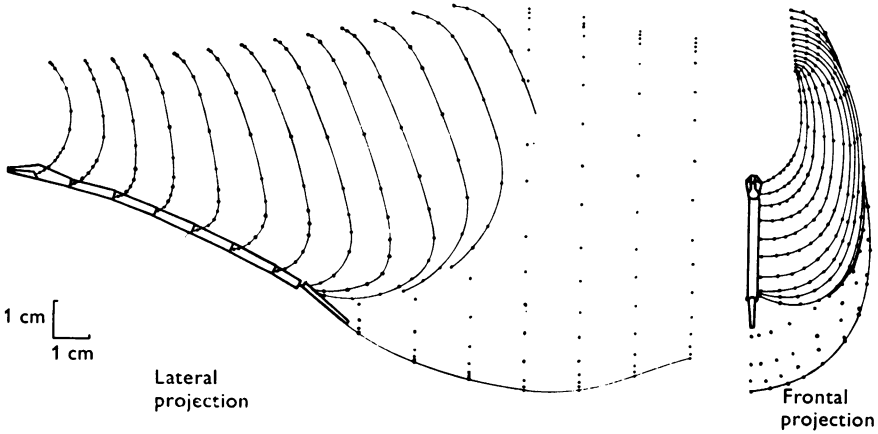

Fig. 4. Lateral (left) and frontal view of the ribs, sternum and abdominal wall obtained by fitting these structures to the set of markers shown in Fig. 3; the dots show the large set of points derived for the numerical processing.

These co-ordinates were referred to a system of three orthogonal axes consisting of the XX- and YY-axes defined above and a ZZ-axis which is normal to both of them and coincides with the optical axis of the camera. Fig. 3 shows the three planar XY (lateral), XZ (dorsal) and YZ (frontal) projections of the set of markers for a given frame of the cine-film.

The final step in the analysis of the photographic records was the 'fitting' of a line to each rib intended to represent the middle of the external surface of each rib; this procedure was necessary in order to correct for the imperfect alignment of the markers on the surface of each rib. Although this was done by eye there was always sufficient information from the three projections and from the measurements made directly on the ribs to reconstruct faithfully the trajectories of each rib. A similar procedure was used to optimize the drawing of several cross-sections of the abdominal wall. When this fitting of the structures was completed they were re-defined by a new and larger set of points, as illustrated in Fig. 4, which was then digitized to constitute the final data describing the ribs, sternum and the abdominal wall.

RESULTS

Changes in configuration during spontaneous breathing

The changes in shape occurring in spontaneous breathing illustrated in Figs. 5, 6 and 7, were analysed from the film frames taken at the extremes of rib cage and abdominal wall motion in inspiration and expiration, respectively. Under the general experimental conditions described, these animals were characterized by active movements of the rib cage, diaphragm and abdominal wall. Surface electromyography confirmed that

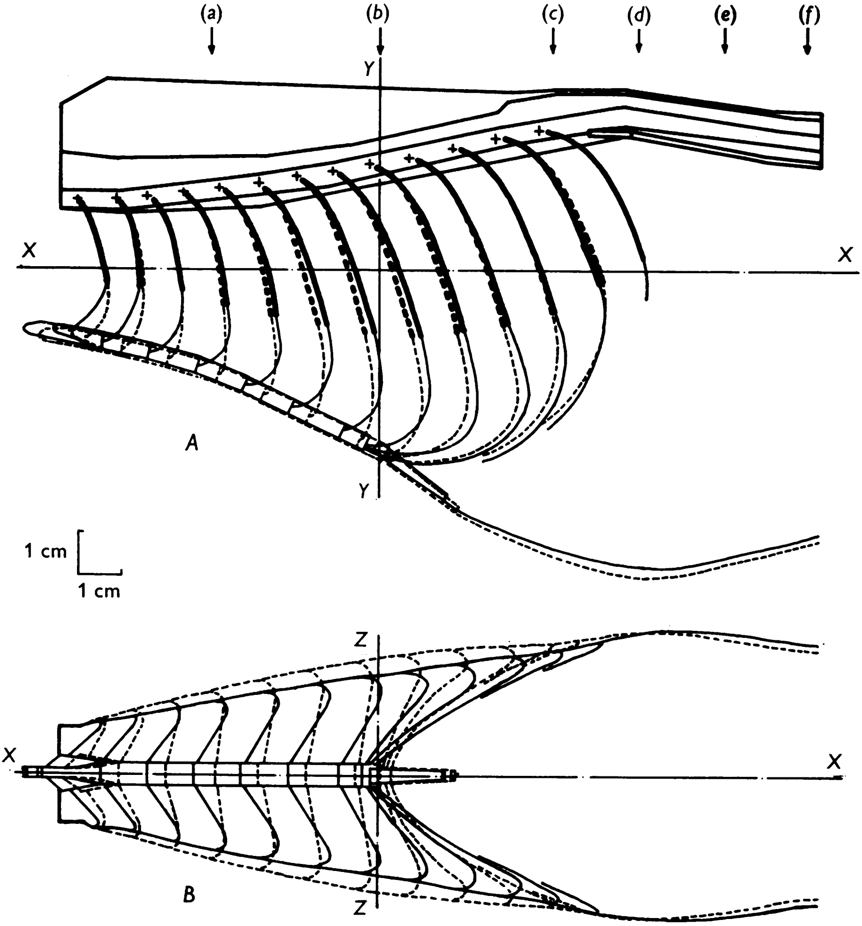

Fig. 5. Spontaneous breathing: comparison between *A*, the lateral and *B*, ventral views of the rib cage and abdomen in the extreme positions of expiration (continuous line) and inspiration (interrupted line). The ventral view was drawn assuming perfect symmetry of the body. (*a*)–(*f*) show the levels of vertical cross-sections shown in Fig. 6.

expiratory (internal intercostal and rectus abdominis) as well as inspiratory (parasternal and external intercostal) muscles were active. Such a distribution of activity is invariably the case for the lightly anaesthetized animal, suspended *prone*, in the considerable experience of one of us (T.A.S.).

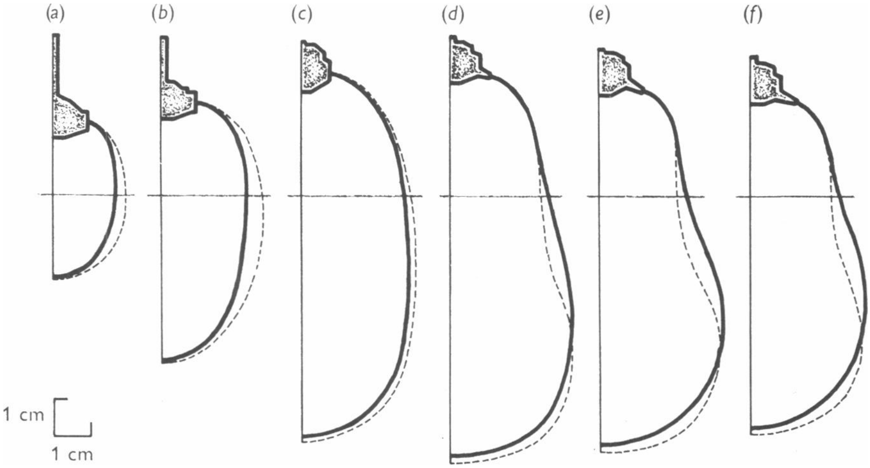

Fig. 6. Spontaneous breathing: vertical cross-sections taken at the levels (*a*), (*b*), (*c*), (*d*), (*e*) and (*f*) defined in Fig. 5 and referring to the extreme positions of expiration (continuous line) and inspiration (interrupted line).

The rib movements responsible for the inflation of the rib cage in inspiration consisted of a rotation outwards and forwards about the costovertebral joints which increased the transverse dimensions of the rib cage all along its length (note that Figs. 5 and 6(*d*–*f*) are cross-sections through the abdomen) but had little effect on its antero-posterior dimensions (Fig. 6(*a*–*c*)). These rib movements have their greatest amplitude from T4 to T11, as best seen in the shape changes derived by stereophotography (Figs. 5 and 6) although they are also visible in the dorsal radiographs (Fig. 7).

Perhaps the most unexpected result of all, was the change in rib cage configuration which occurs anteriorly in the region of the sternum and costal cartilages during spontaneous breathing. The inspiratory movement of the ribs was associated with a widening of the angle between the sternum and each of the costal cartilages which resulted in a clear cut *caudal* displacement of the sternum. In the moving cine-film this effect was quite dramatic, the rostral part of the anterior chest wall appearing to move independently about the trajectories traced by the costal tips of the ribs. As viewed laterally (e.g. Fig. 5*A*), the costal cartilages appeared to straighten out so that their motions with respect to the tips of the ribs resembled those of extension at the elbow.

At full inspiration, the entire length of the ventral abdominal wall was displaced downwards, the movement being most apparent at the lowest point of the pendant abdomen. This downward motion of the ventral abdominal wall was accompanied by an inward motion of the lateral, dorsolateral abdominal wall (Fig. 6 (*d–f*)) which was maximal at about the level of the dorso-ventral mid-point.

In the expiratory phase, the rib cage was characterized by a caudal displacement of the ribs and a forward position of the diaphragm. The ventral abdominal wall was in an elevated position and this was accompanied by an outward movement of the dorso-lateral and lateral regions of the abdominal wall, so that in the transverse view (Fig. 6) the dorsal part of the abdomen appears in an 'inflated' position.

Figs. 7*A* and 8 illustrate tracings of the dorsal and lateral X-ray plates taken during spontaneous breathing at the height of inspiration and expiration and clarify the movements of the diaphragm and viscera. During inspiration, the traces show a smooth diaphragm surface and an apparent clockwise rotation of the liver which must be a consequence of the fact that most of the diaphragmatic pull is applied to the dorso-cranial surface of this organ. This movement of the liver contributes to the downward movement of the ventral abdominal wall during the inspiratory phase, a process aided by the active inhibition of expiratory motoneurones and hence of abdominal tone at this time (cf. Sears, 1964).

Artificial ventilation

In view of the concepts underlying the pressure–volume analysis we were particularly interested in defining the relaxation configuration of the respiratory system and the changes in shape which occur during artificial respiration.

Immediately following the film sequences of spontaneous breathing the animal was paralysed with Flaxedil and artificially ventilated at the same tidal volume as recorded by the spirometer. The records were analysed in the same way and the results obtained illustrated in Figs. 7*B*, 9 and 10.

In the expiratory phase of the pump the rib cage and abdomen adopted a configuration characterized particularly by a fully pendant abdomen due to the loss of tone in the abdominal and rib cage muscles. This loss of tone allowed the weight of the viscera to deform the abdomen and rib cage, increasing their dorso-ventral dimensions while decreasing their transverse dimensions, thus forcing the trunk into a configuration which

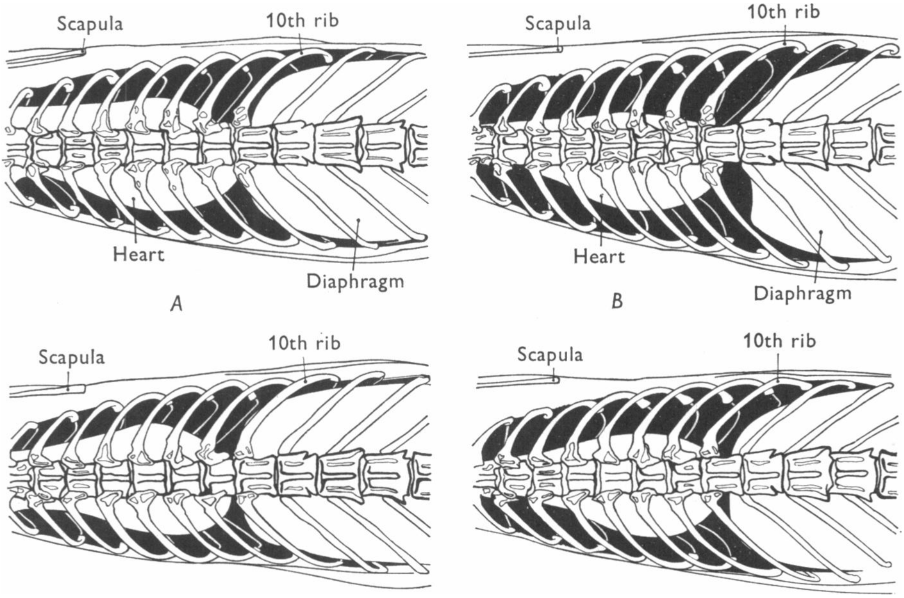

Fig. 7. Tracings of X-ray plates showing the partial dorsal views of the trunk in peak inspiration (top) and peak expiration (bottom) for *A*, spontaneous breathing and *B*, artificial ventilation.

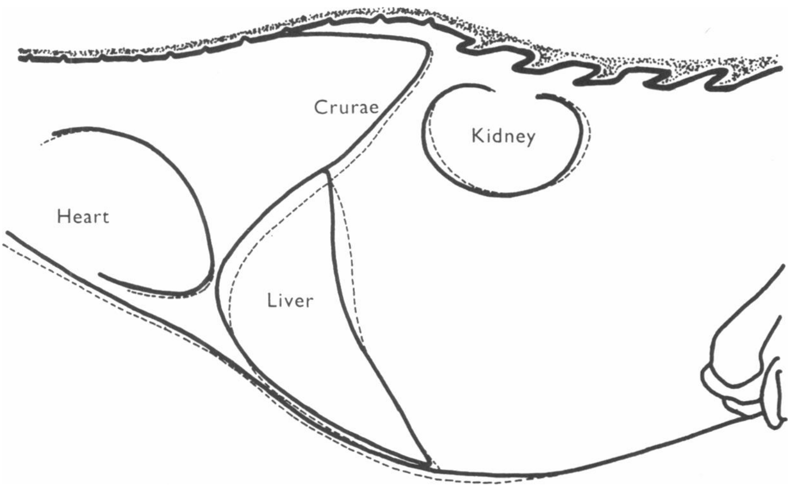

Fig. 8. Spontaneous breathing: tracings of X-ray plates showing lateral views of the trunk in peak expiration (continuous line) and peak inspiration (interrupted line).

was completely distinct from that occurring at end expiration during spontaneous breathing.

Only small movements of the sternum occurred during artificial ventilation. The ribs moved outwards and forwards during lung inflation but

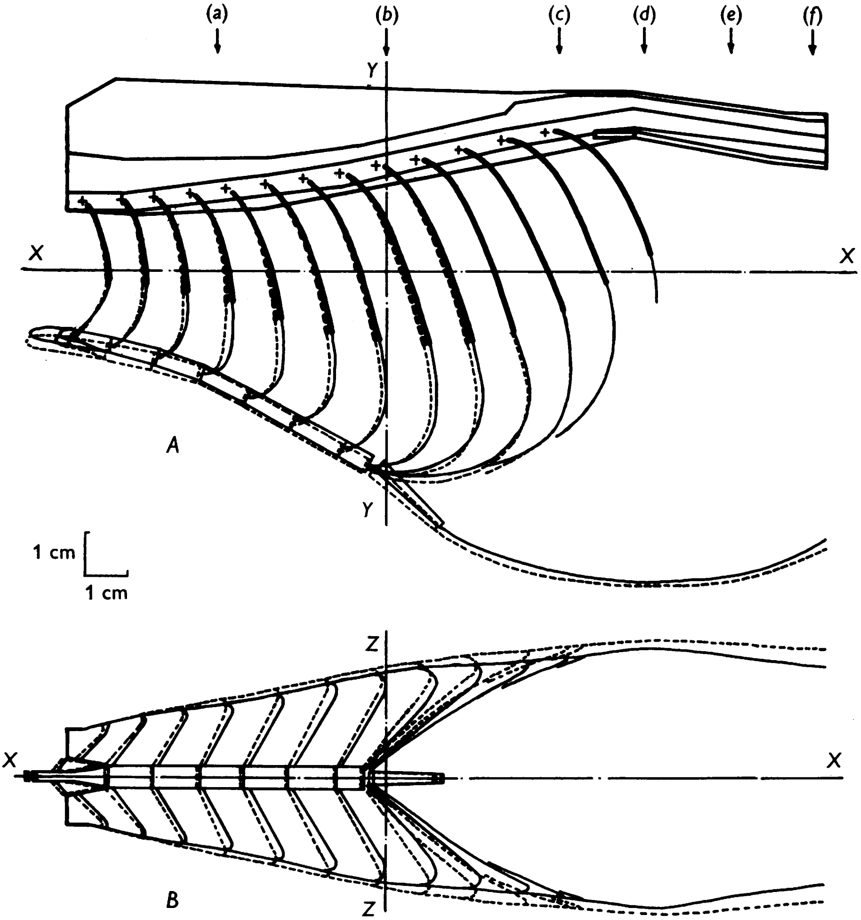

Fig. 9. Artificial ventilation: comparison between *A*, the lateral and *B*, ventral views of the rib cage and abdomen in the extreme positions of expiration (continuous line) and inspiration (interrupted line).

both views in Fig. 9 show quite clearly that the sternum actually moved forwards, i.e. in the opposite direction to that which occurred in the inspiratory phase of spontaneous breathing. The tracings in Figs. 7*B* and 10 showed clearly that for the same tidal volume the diaphragm undergoes a more pronounced excursion than it does in spontaneous breathing, indicating that the complete loss of muscle tone makes the abdomen more compliant than the rib cage. The shape of the diaphragm at peak inflation is also seen to be appreciably distorted (Fig. 7*B*) suggesting an unnatural displacement of the abdominal viscera.

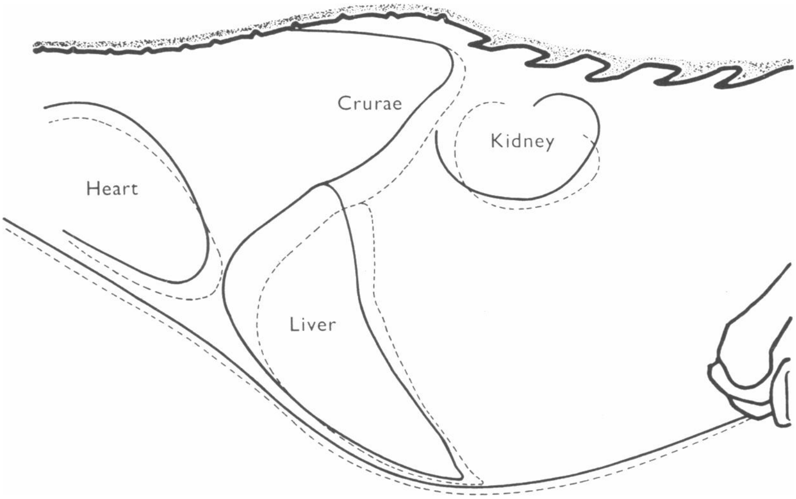

Fig. 10. Artificial respiration: comparison between the X-ray tracings of lateral views of the peak expiration (continuous line) and peak inspiration (interrupted line).

Comparison between spontaneous and artificial ventilation

The individual changes in configuration of the rib cage and abdomen during spontaneous breathing and artificial ventilation described above are directly compared in the superimposed drawings of Figs. 11, 12 and 13. These clearly emphasize the more elevated position of the abdomen during spontaneous breathing, both in inspiration as well as in expiration and the corresponding differences in the lateral abdominal wall. Secondly, they emphasize the opposite motions of the sternum in inspiration for the two conditions. The caudal displacement of the sternum in inspiration during spontaneous breathing can only be understood mechanically as a straightening of the costal cartilages in response to activity of the interchondral muscles; the mechanical action of the latter is dependent, in turn, on the trajectories of the ribs resulting from intercostal muscle activity which in quiet breathing occurs in the proximal parts of the intercostal space.

Although the radiographs for spontaneous and artificial ventilation cannot be directly superimposed, because the position of the X-ray camera was not exactly the same in both cases, Figs. 8, 10 and 13 suggest that under paralysis the diaphragm moves between extreme configurations which, for the prone position, are further apart and located more caudally than the corresponding positions in spontaneous breathing. This finding is consistent with the lower position taken by the ventral surface of the rib cage and abdomen (cf. Fig. 11) which necessarily must correspond to a displacement of the abdominal viscera in a caudo-ventral direction. The rib cage was less compliant than the diaphragm–abdomen combination and behaved as if it took a smaller share of the tidal volume. In the case of spontaneous breathing, on the other hand, the independent but opposite motions of the ventral and lateral abdominal walls were coupled with rib

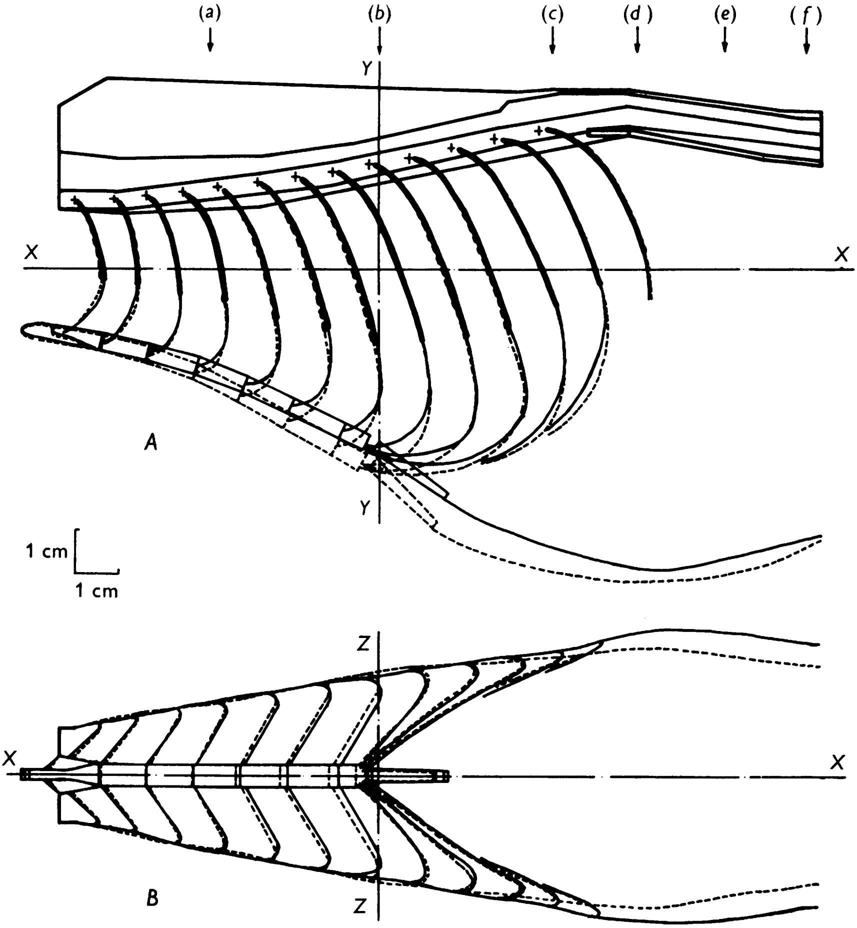

Fig. 11. Comparison of the extreme position of expiration in spontaneous (continuous line) and artificial (interrupted line) ventilation: *A*, lateral and *B*, ventral views.

cage motions which exceeded and virtually contained those corresponding to artificial ventilation, indicating that in the former case a relatively greater share of the tidal volume is taken by the rib cage.

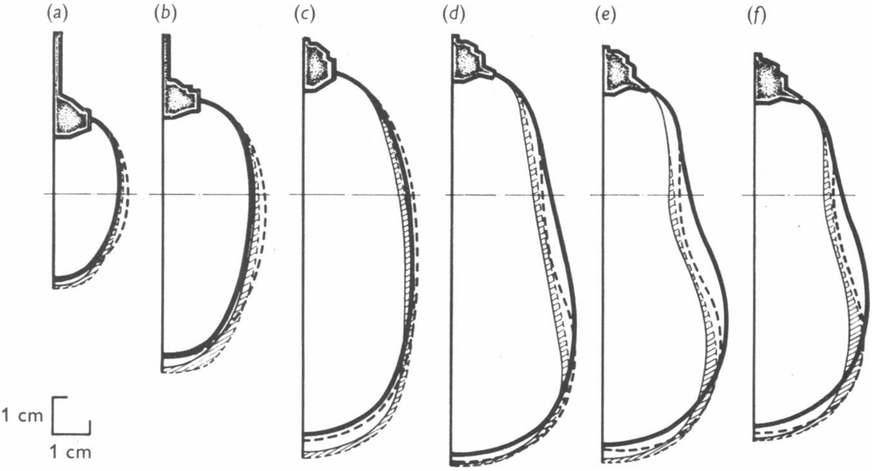

Fig. 12. Comparison between spontaneous (heavy lines) and artificial (finer lines) ventilation: vertical cross-sections at the levels (*a*), (*b*), (*c*), (*d*), (*e*) and (*f*) shown in Figs. 5 and 9. Extreme positions of expiration (continuous lines) and inspiration (interrupted lines).

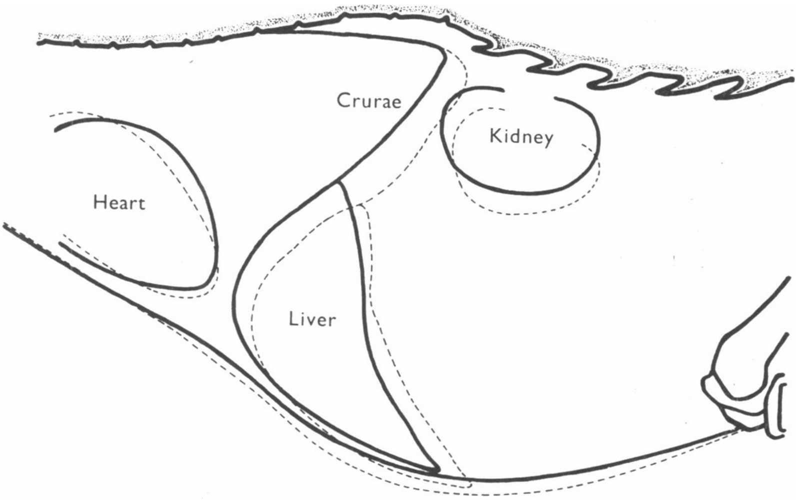

Fig.13. Comparison of lateral X-ray tracings for the position of peak inspiration in spontaneous (continuous line) and artificial (interrupted line) ventilation.

DISCUSSION

This work was undertaken to clarify the nature of the movements of structures which participate in the respiratory movements. Such knowledge is required if their performance is to be understood from a mechanical point of view, as that of structural elements whose load resisting properties are dependent on their three-dimensional shape. We have achieved this result with a reasonable accuracy for the surfaces of the rib cage and a major part of the abdominal wall in prone, anaesthetized cats.

The photographic method met the need both for recording movement in large areas of the photographic field and the large depth of field resulting from the steep inclination of the dorsal and ventral surfaces of the body relative to its lateral surface. The mirror system allowed the acquisition of stereometric data with a single camera and provided simultaneous photographs of the dorsal, lateral and ventral regions of the body. The use of markers to define the body surfaces instead of the level contours produced by the methods of conventional photogrammetry (Beard & Burke, 1967; Miskin, 1956) arose from our need to use general purpose graphic and computational facilities. As described in the Appendix, the centre of the base of any marker could only be specified as a sphere of mean radius 0·24 mm centred at the true position of the point. This limit of accuracy is the result of the combined influence of the optics of the camera, the large size of the markers needed for adequate visibility, the imprecisions of the photographic set-up and the limitations in the processing of the stereometric data. It must however be emphasized that the quantification of the trunk wall movements involves not only the changes in configuration of the exposed surface of the body but also those of structures such as the ribs, cartilages and muscles which are partially or completely buried under that surface. This limits the accuracy with which the shape and position of the structure can be defined and justified the photogrammetric method. Finally, while fully recognizing the traumatic consequence of the extensive dissection which was necessary to place the markers on the ribs and abdominal wall we were able to verify by radiography in intact anaesthetized animals that the movements of these structures were of the same nature as those recorded in our preparations.

The salient features of the spontaneous inspiratory movements were the straightening of the costal cartilages (under the action of the interchondral muscles), the widening of the angles they make with the sternum at the sternochondral joints and the caudal displacement of the sternum. These deformations, which are readily apparent in the cat due to the length of the costal cartilages, are intimately related to the movements of the ribs. The axes of rotation at the costovertebral joints are such that the inspiratory movements of the ribs are simultaneously forward and outward and are associated with a reduction in the eccentricity and a consequent increase in area of the nearly elliptical cross-section of the rib cage throughout its length. Because the ribs do not bend appreciably (Da Silva, 1971) the change in shape arising from the movements of the costal cartilages and sternum form an essential mechanical feature which permits the rib movements to achieve maximum transverse rib cage dimensions for a given degree of rib rotation; these movements thus contribute positively towards the efficiency of the rib cage performance.

The increase in thoracic volume recorded in spontaneous breathing resulted from the combined movements of the rib cage and diaphragm; the former involved the activity both of the intercostal muscles, which elevate the ribs and the parasternal or interchondral (internal intercostal) muscles (Bronk & Ferguson, 1934) which appear to be the main cause of the caudal movement of the sternum. The inflation of the rib cage is accompanied by the inflation of the lower cranial region of the abdomen, caused by the pressure exerted on the abdominal viscera by the diaphragm, the inhibition of tone in the expiratory muscles and the slight elevation of the lower costal cartilages (cf. D'Angelo & Sant'Ambrogio, 1974). The liver is closely related by ligaments to the diaphragm and to the cranio-ventral region of the abdominal wall. This coupling clearly contributes to the diaphragm actions on the remaining abdominal viscera and vice versa as well as the lower rib cage. Under compression, the concave caudal surface of the lobed liver will be forced open pushing its lateral surface against the rib cage and abdominal walls, thus stabilizing them against local inward directed transverse forces. It is not implied that this is the only mechanism involved. D'Angelo & Sant'Ambrogio (1974) have shown that the increase in transverse diameter of the lower rib cage caused by the diaphragm's contraction (phrenic nerve stimulations) also occurs in the eviscerated rabbit and dog. Nevertheless, such action entirely depended on the position of the dome of the diaphragm, these forces on the lower rib cage being directed outwards when the dome was mechanically restrained in a high position but directed inwards when the dome was free to move to a lower position. In the intact animal, therefore, the stabilized position of the liver beneath the diaphragm is likely to play a significant role in the distribution of the forces developed by the diaphragm. Certainly this could explain the rotatory movement of the liver observed in the lateral X-ray tracings of both spontaneous and artificial inspiratory movements.

The caudal edge of the rib cage is formed by the thirteenth rib, the ninth to thirteenth costal cartilages and the xiphoid process. To this boundary are attached passive structures such as the linea alba, the lumbodorsalis fascia, the aponeurosis of the abdominal muscles, and the muscles themselves, the diaphragm, transversus abdominis, obliquus abdominis internus, quadratus lumborum, retractor costae ultimae muscles and the last digitation of the serratus posterior muscle. Except for the diaphragm, all these structures contribute to the creation around the entire edge of the rib cage of a tangential pull in a caudad direction which prevents the lower intercostal spaces from closing up under the action of the associated intercostal muscles. Thus Hoover (1922) showed that if the attachments of the abdominal muscles to the rib cage are severed in the dog, the costal borders move markedly laterally during inspiration. This movement, which is mainly caused by the contraction of the boundary muscles with vertebral insertions, may represent the only mechanism for keeping the lower intercostal spaces open and taut; it certainly illustrates the complex nature of the forces applied to this boundary of the rib cage. The contraction of the diaphragm produces a pull, also tangential to the caudad edge of the cage but moving it in a craniad rather than caudad direction. The forces developed by the other boundary muscles and structures must therefore be capable of immobilizing the caudad rim of the cage against the combined action of the diaphragm and intercostal muscles; the equilibrium of the transverse components of all these boundary forces is necessarily mediated by the support provided by the liver and resulting from the mechanism outlined above.

The foregoing arguments suggest a need for some activity of rib cage and abdominal muscles throughout the respiratory cycle, both in inspiration, when the lung recoil forces transmitted to the caudad boundary of the rib cage by the diaphragm are greatest and the sternum moves further caudad; and in expiration, when the ribs are pulled towards the sagittal plane of the animal and the caudal edge of the cage moves in a caudad direction. Thus some light is shed on the possible function of tonic electromyogram activity which can be recorded from the thorax (Massion, Meulders & Colle, 1960; Duron, 1966) and abdominal wall particularly in the vicinity of the diaphragm's insertion (T. A. Sears, unpublished). Tonic activity of the respiratory muscles is usually given the label 'postural', having an implicit identity with the postural activity of the limb muscles. However, the foregoing arguments point to a more specific role for tonic activity in optimizing the mechanical performance of the rib cage and abdomen. Although such muscular activity affects and controls the elastic properties of the abdominal wall, the movements of this wall are determined basically by its mechanical coupling to the vertebral column, the rib cage and the liver and by the fluid-like behaviour of the abdominal contents.

The silencing of the respiratory muscles under Flaxedil led to marked changes in the shapes of the rib cage and abdomen both of which became pendant and narrower. For this reason the ranges of trunk wall configurations which corresponded to the movements of spontaneous and artificial ventilation were clearly distinct. This narrowing of the rib cage almost certainly reflects the 'expiratory' effect on rib cage volume exerted by the gravitational pull on the abdominal viscera unsupported by abdominal muscle tone (cf. Agostoni, D'Angelo & Bonanni, 1970; Agostoni & D'Angelo, 1971); however, we did not attempt a simultaneous analysis of the changes in pleural and abdominal pressures consequent on neuromuscular blockade to verify this. This finding also indicates that with the anaesthetized cat in the prone (suspended) position (and presumably under natural conditions in the standing animal) some rib cage and abdominal muscle activity must persist throughout the cycle; such activity, which should by no means be specific for the particular postural circumstances involved in our experiments, could enable the rib cage to preserve its shape in the face of the applied loads. A familiar example of the relationship between the shape of a thin shell-like structure and its efficiency in handling loads is the egg shell which, when intact, can resist the application of a surface pressure many times larger than the slight bending effort needed for breaking a small isolated piece of its wall. The rib cage is a shell-like structure and consequently its mechanical performance is closely tied-up with its three-dimensional configuration (cf. Konno & Mead, 1967); in particular, the smoother is its shape the better behaved and safer will tend to be the distribution of stress in its elements for a given load (Flügge, 1960); large values of local surface curvature could cause exaggerated bending movements and stresses which not only endanger the physical integrity of the structure but would need to be equilibrated with increased muscular activity and hence increase the work of breathing. Thus considerations of safety and efficiency lead to the need for optimal configurations of the rib cage which the animal could achieve through the servo control of its muscles (see Sears, 1973); and when the rib cage performs movements its shape evolves through a range of configurations all of which must be capable of handling adequately the prevailing transmural and boundary loads.

The need for muscular activity to satisfy demands of purely structural character, based on the results of using neuromuscular blockade, as argued above, is again supported by the change in the rib cage shape which occurs with other forms of paralysis. Experiments of multiple intercostal neurectomy in dogs (Alexander, 1929) showed that in quiet inspiration the inactivated side of the partially silenced rib cage sinks in paradoxically with the consequent distortion of its shape. Similar results were reported in man (Bonomo, 1927; Hoover, 1922) and confirmed by one of us in the cat (T. A. Sears, unpublished). Such paradoxical movement is of course familiar in a high spinal transection which leaves diaphragmatic excitation intact; and in deep anaesthesia when the rib cage muscles are inactive and diaphragmatic movements alone cause the tidal movement of air. In this latter case, the combination of rib cage paradoxing and a highly compliant abdominal wall lead to a much greater shortening of the diaphragm and hence to a reduction in its mechanical efficiency (cf. Marshall, 1962; Pengelly *et al.* 1971; Mead, 1973).

These facts suggest that an appreciable amount of muscular activity associated with respiration is directly related to the task of guaranteeing the structural stability of the rib cage shell to optimize the piston-like action of the diaphragm. It is therefore not surprising, as emphasized by Agostoni, Campbell & Freedman (1970), that measurements of the efficiency of breathing have given such divergent results (see also Konno & Mead, 1967). Failure by these muscles to meet this requirement could lead to a deterioration of the conditions in which the lungs perform and may produce some of the symptoms traditionally identified with cases of pathological changes in airway resistance or lung compliance or indeed, give rise to the possibility of pathology as suggested in the case of diaphragm paralysis (Newsom Davis, Goldman, Loh & Casson, 1976).

The authors are indebted to Messrs J. W. Green, R. D. Puddy, R. L. Moore and W. C. Cuttler of the Imperial College of Science and Technology for their technical help. Messrs A. H. Prentice and R. E. Brooks of the Institute of Neurology are thanked for undertaking the cinematography. This work is partially supported by a grant from The Medical Research Council which is gratefully acknowledged.

APPENDIX

The diagram of Fig. 14 represents the basic geometry of the mirror system used in the experiments to produce stereophotography. In this diagram P_0 (x_0, y_0, z_0) is a point on the object to be photographed; P_2 (x_2, y_2, z_2) is its image as seen from the camera and P_1 (x_1, y_1, z_1) the trace on the mirror surface of the ray $\overline{NP_2}$. Q_0 and Q_1 are the images of P_0 and P_2 (and P_1), respectively, on the image plane of the lens system. The co-ordinates of a point object P_0 photographed with this system may be deduced from those of W_1 (x_3, y_3) and W_0 (x_4, y_4) situated on the plane $z = 0$ and corresponding to the images Q_1 and Q_2 respectively. The values of those co-ordinates are as follows:

$$x_0 = x_3(1-z_0/L),$$

$$y_0 = y_3(1-z_0/L),$$

$$z_0 = [z_1-G.(y_3-by_4)].[1-G.(y_3/L)]^{-1},$$

where:

$$G = [(1-a^2).(L-z_1)-2a.y_1].[(1-a^2).y_1+2q.a(L-z_1)]^{-1},$$

$$a = \tan x,$$

and $b = [aL-H].[aL-|y^4|]^{-1}$ in which the parameter H takes the appropriate value H_1 or H_2, the symbol $|\ |$ stands for absolute value and $q = +1$ for the top mirror and $q = -1$ for the bottom mirror. The co-ordinates of W_1 and W_0 are deduced from those of Q_1 and Q_0, respectively, on the photographic record through the multiplication by the corresponding scaling factor as obtained by calibration.

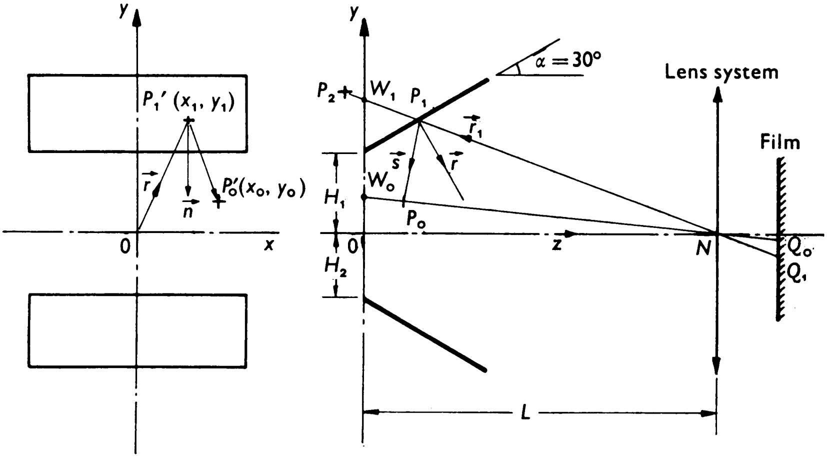

Fig. 14. Geometry of the photographic system: L, distance from the bottom edge of the mirrors to the axis of the lens system; N, nodal point of this system, H_1 and H_2, distance of the internal edge of each mirror to the axis of the lens system; α, angle made by the plane of the surface of the mirrors with the lens axis; $\vec{r} = \overline{NP_1}$; $\vec{s} = \overline{P_1P_0}$; $\vec{n}$ = normal to the mirror surface at P_1. P_0 is a point on the object to be photographed; P_2, its image as seen from the camera; P_1, the trace on the mirror surface of ray $\overline{NP_2}$. Q_0 and Q_1 are the images of P_0 and P_2 and W_0 and W_1 corresponding points on the plane $z = 0$.

The whole photogrammetric system including all the computations and graphical processing was applied to a specially prepared hollow brass cylinder for calibration purposes. The cylinder was 270 mm long, its external surface was accurately machined to a nominal diameter of 98 mm and black anodized; sixty reflective markers of the type described in Methods were glued to this external surface at the crossing points of ten equidistant longitudinal lines and six equidistant parallel circles drawn on a 240 mm central region. The cylinder was positioned in the animal frame and photographed. The complete processing of the corresponding photographic data yielded the position, referred to the mirror system, of the markers which were visible to the camera; the external surface of the cylinder as well as the longitudinal lines and the parallel circles were then graphically fitted to those marker points and the radius of the cylinder was determined. From these results it was found that the errors in locating the base centre of the markers with regard to their exact positions showed no detectable directional bias and, when treated as distance moduli, showed a distribution characterized by a mode of 0·20 mm, a mean of 0·24 mm and standard deviation of 0·19 mm.

REFERENCES

AGOSTONI, E., CAMPBELL, E. J. M. & FREEDMAN, S. (1970). Energetics. In *The Respiratory Muscles*, ed. CAMPBELL, E. J. M., AGOSTONI, E. & NEWSOM DAVIS, J., London: Lloyd Luke.

AGOSTONI, E. & D'ANGELO, E. (1971). Topography of pleural surface pressure during simulation of gravity effect on abdomen. *Resp. Physiol.* **12**, 102–109.

AGOSTONI, E., D'ANGELO, E. & BONANNI, M. V. (1970). The effect of the abdomen on the vertical gradient of pleural surface pressure. *Resp. Physiol.* **8**, 332–346.

ALEXANDER, J. (1929). Multiple intercostal neurectomy for pulmonary tuberculosis. *Am. Rev. Tuberc. pulm. Dis.* **20**, 637–684.

BEARD, L. F. H. & BURKE, P. H. (1967). Evolution of a system of photogrammetry for the study of facial morphology. *Med. biol. Illust.* **17**, 20–25.

BONOMO, V. (1927). La resezione dei nervi intercostali nella cura chirurgica della tubercolosi pulmonare. *Annali. ital. Chir.* **6**, 1199–1214.

BRONK, D. W. & FERGUSON, L. K. (1934). The nervous control of intercostal respiration. *Am. J. Physiol.* **110**, 700–707.

D'ANGELO, E. & SANT'AMBROGIO, G. (1974). Direct action of contracting diaphragm on the rib cage in rabbits and dogs. *J. appl. Physiol.* **36**, 715–719.

DA SILVA, K. M. C. (1971). Neuromuscular activity and respiratory dynamics in the cat. Ph.D. Thesis, University of London.

DURON, B. (1966). Role comparatif des divers muscles thoraciques du Chat dans la respiration, la posture et le frisson thermique. Etude electromyographique. *J. Physiol., Paris* **58**, 514.

EULER, C. VON (1973). The role of proprioceptive afferents in the control of respiratory muscles. In a symposium *Neural Control of Breathing. Acta neurobiol exp.* **33**, 329–341.

FLÜGGE, W. (1960). *Stresses in Shells*. Berlin: Springer-Verlag.

HOOVER, C. F. (1922). The function and integration of the intercostal muscles. *Archs intern. Med.* **30**, 1–33.

KONNO, K. & MEAD, J. (1967). Measurements of separate volume changes of rib cage and abdomen during breathing. *J. appl. Physiol.* **22**, 407–422.

KONNO, K. & MEAD, J. (1968). Static volume–pressure characteristics of the rib cage and abdomen. *J. appl. Physiol.* **24**, 544–548.

MARSHALL, R. (1962). Relationships between stimulus and work of breathing at different lung volumes. *J. appl. Physiol.* **17**, 917–921.

MASSION, J., MEULDERS, M. & COLLE, J. (1960). Fonction posturale des muscles respiratoire. *Archs int. Physiol. Biochim.* **69**, 314–326.

MEAD, J. (1973). Implications of internal loading to breathing in man. *Acta neurobiol. exp.* **33**, 343–354.

MISKIN, E. A. (1956). The application of photogrammetric techniques to medical problems. *Photogramm. Rec.* **2**, 92–110.

NEWSOM DAVIS, J., GOLDMAN, M., LOH, L. & CASSON, M. (1976). Diaphragm function and alveolar hypoventilation. *Q. Jl Med.* **45**, 87–100.

PENGELLY, L. D., ALDERSON, A. M. & MILIC-EMILI, J. (1971). Mechanics of the diaphragm. *J. appl. Physiol.* **30**, 797–805.

RAHN, J., OTIS, A. B., CHADWICK, L. E. & FENN, W. O. (1946). The pressure–volume diagram of the thorax and lung. *Am. J. Physiol.* **146**, 161–178.

SEARS, T. A. (1964). The slow potentials of thoracic respiratory motoneurones and their relation to breathing. *J. Physiol.* **175**, 404–424.

SEARS, T. A. (1973). Servo control of the intercostal muscles. In *New Developments in EMG and Clinical Neurophysiology*, vol. 3, ed. DESMEDT, J. E., pp. 401–417, Brussels: S. Karger.