hypothesis that the increase in the A-V difference in Pi and the decrease in force is due to a breakdown of these ATP

ic effects of hypoxia on the force of contraction in seven dogs (Table 3). These muscles were stimulated at 1

The paper continues with a detailed discussion of the effects of hypoxia on muscle function, highlighting the differences observed and the implications for respiratory regulation. It concludes with references to previous studies and future directions for research in this area.
portionately by the coordinated action of the abdominal and rib cage muscles. In shifting from recumbency to the upright, FRC and end-inspiratory volume increase substantially, the diaphragm is shortened less than it otherwise would be through the tonic contraction of abdominal muscles. Secondly, to the extent that diaphragmatic operating length is not completely defended, an additional mechanism increases diaphragmatic excitation without changes in chemical drive. The basis for this diaphragmatic facilitation is not known, but the fact that it is clearly demonstrable in patients with high cervical chord transections suggests that it is autogenic and a reasonable possibility is that tendon receptors in the diaphragm are involved.

The strength of these mechanisms is indicated by the well-established fact that the arterial Pco₂ of spontaneously breathing healthy subjects is maintained, or if anything tends to decrease, as operating lung volume is increased over a wide range from recumbency to positive pressure breathing in the upright posture. Thus, mechanical loading and mechanical disadvantages are compensated by highly dissimilar mechanisms. Mechanical loading is normally dealt with at a conscious level: we avoid mechanical loads, or do something about them, and when we cannot, we see a doctor! We do not have effective homeostatic mechanisms to compensate for mechanical loads beyond the stabilizing influence of the respiratory system’s substantial internal impedance.

In contrast, changes in mechanical advantage are dealt with automatically and efficiently. So efficiently, indeed, that we have failed until recently to recognize that such mechanisms exist. These distinctions have important implications to tests of ventilatory regulation. Conscious responses are a natural and highly variable component of mechanical loading. Only in their absence can we expect that mechanical loading will depress ventilation. In contrast, the responses to changes in mechanical advantage are automatic and efficient. When in the course of lung diseases the operating lung volume increases, these mechanisms should at first be adequate, but at some point they should be taxed to their limit. Blood gases should remain normal until tidal volume encroaches upon these limits.

Recent data on intercostal muscle function, largely electromyographic, tend to confirm the ideas of Hamberger, who, in 1748, proposed a theory of intercostal muscle action upon the rib cage. Hamberger’s scheme was based upon a consideration of the ribs as levers and the vertebral column and sternum as fulcra, and of the directions in which the internal and external intercostal muscle fibers ran. He proposed that the external intercostals were inspiratory and that the internal intercostals were expiratory, except in the parasternal regions where the internal intercostals (there are no other intercostal muscles) are inspiratory. Careful selective electromyographic studies in both animals and man (using small bipolar needle electrodes) by Draper et al, Taylor et al, and Sears et al have amply confirmed Hamberger’s ideas.

During quiet breathing, it is generally acknowledged that the diaphragm is the principal driver of respiration. However, there is resting inspiratory activity in parasternal intercostals in the upper few interspaces, and in the scaleni. Expiratory activity is present in the lower internal intercostals. In cervical quadriplegics where upper intercostal action is absent, upper thoracic paradoxing on inspiration is regularly seen. This is not seen in normal adults. With increase in the depth and vigor of respiratory efforts, inspiratory activity increases in the external intercostals which are recruited from above downward. Activity also increases in the internal intercostals which are recruited from below upward. Scalenus activity also increases and activity appears in the sternomastoid and trapezius muscles with larger breaths. At near-maximal inspiration, the pectorals, serratus and many of the back muscles also become active. The abdominal muscles show little activity during quiet breathing in the supine position. However, in the upright posture both inspiratory and expiratory activity is usually present. The expiratory activity, in particular, increases with deeper and faster breathing. Recent work of Mead and Goldman emphasizes the importance of abdominal muscles and of abdominal pressure as a principal force driving the rib cage. Their investigations suggest that the functional organization of both the abdominal and rib cage muscles acts to optimize the function of the diaphragm with respect to its length-tension and force-velocity characteristics.

Mechanical Functions of Respiratory Muscles

The integrated electromyogram, which can be integrated and expressed in any one of several ways (see other articles in this issue) is generally related to the metabolic activity of the muscle. Although several studies have shown this, a recent study of Bigland-Ritchie done on the human quadriceps femoris muscles, illustrates a linear relationship between the integrated electromyogram and the oxygen uptake, generally accepted as an index of metabolic activity.

The translation of this metabolic activity, as indicated by the electromyogram, into mechanical activity (force development and motion) depends upon force-length and force-velocity considerations. The length-tension be-