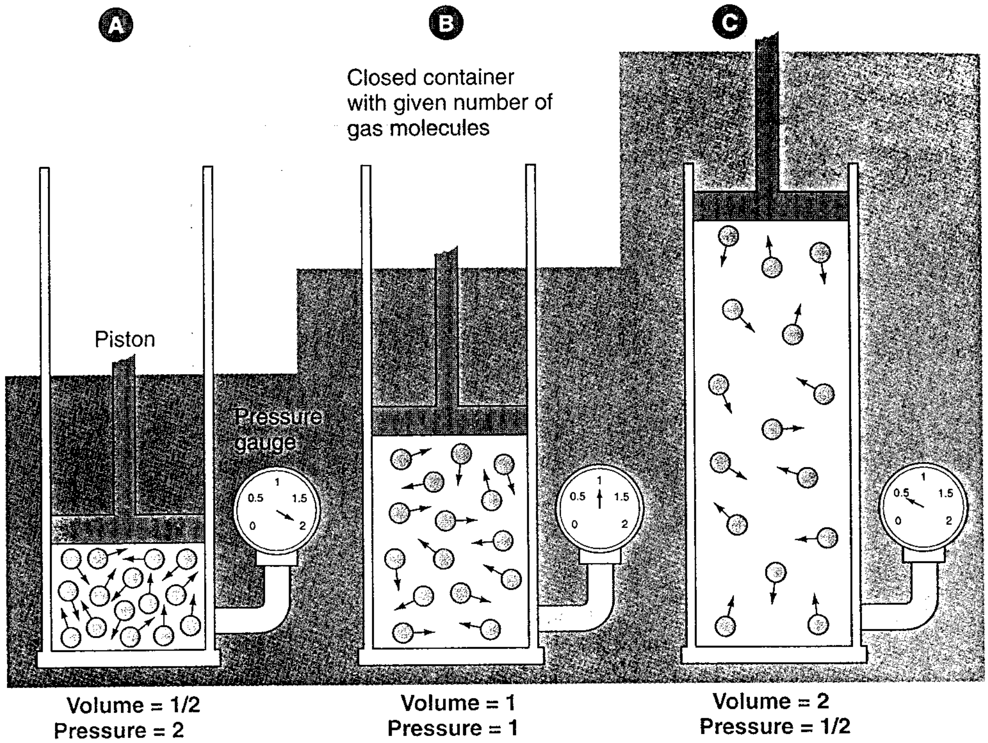
FIGURE 13-10
Boyle's law
Each container has the same number of gas molecules. Given the random motion of gas molecules, the likelihood of a gas molecule striking the interior wall of the container and exerting pressure varies inversely with the volume of the container at any constant temperature. The gas in container B exerts more pressure than the same gas in larger container C but less pressure than the same gas in smaller container A. This relationship is stated as Boyle's law: $P_1V_1 = P_2V_2$. As the volume of a gas increases, the pressure of the gas decreases proportionately; conversely, the pressure increases proportionately as the volume decreases.



act directly on the lungs to change their volume. Instead, these muscles change the volume of the thoracic cavity, causing a corresponding change in lung volume because the thoracic wall and lungs are linked together by the intrapleural fluid's cohesiveness and the transmural pressure gradient.

Let us follow the changes that occur during one respiratory cycle—that is, one breath in (**inspiration**) and out (**expiration**). Before the beginning of inspiration, the respiratory muscles are relaxed, no air is flowing, and intra-alveolar pressure is equal to atmospheric pressure. The major **inspiratory muscles**—the muscles that contract to accomplish an inspiration during quiet breathing—include the *diaphragm* and *external intercostal muscles* (Fig. 13-11 and ▲ Table 13-1, p. 444). At the onset of inspiration, these muscles are stimulated to contract, resulting in enlargement of the thoracic cavity. The major inspiratory muscle is the diaphragm, a sheet of skeletal muscle that forms the floor of the thoracic cavity and is innervated by the **phrenic nerve**. The relaxed diaphragm assumes a dome shape that protrudes upward into the thoracic cavity. When the diaphragm contracts upon stimulation by the phrenic nerve, it descends downward, enlarging the volume of the thoracic cavity by increasing its vertical dimension (Fig. 13-12a). The abdominal wall, if relaxed, can be seen to bulge outward during inspiration as the descending diaphragm pushes the abdominal contents downward and forward. Seventy-five percent of the enlargement of the thoracic cavity during quiet inspiration is attributed to contraction of the diaphragm.

Two sets of **intercostal** (*inter* means "between"; *costa* means "rib") **muscles** lie between the ribs—the external intercostal muscles lie on top of the internal intercostal muscles. Whereas contraction of the diaphragm enlarges the thoracic cavity in the vertical dimension, contraction of the **external intercostal muscles**, whose fibers run downward and forward between adjacent ribs, enlarges the thoracic cavity in both the lateral (side-to-side) and anteroposterior (front-to-back) dimensions. When the external intercostals contract, they elevate the ribs and subsequently the sternum upward and outward (Figs. 13-12a and b). **Intercostal nerves** activate these intercostal muscles.

Before inspiration, at the end of the preceding expiration, intra-alveolar pressure is equal to atmospheric pressure so no air

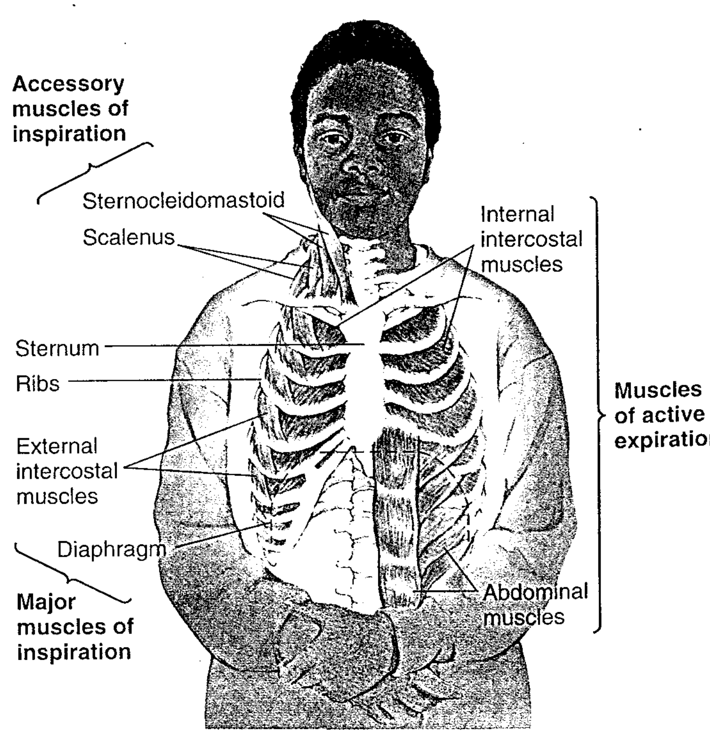
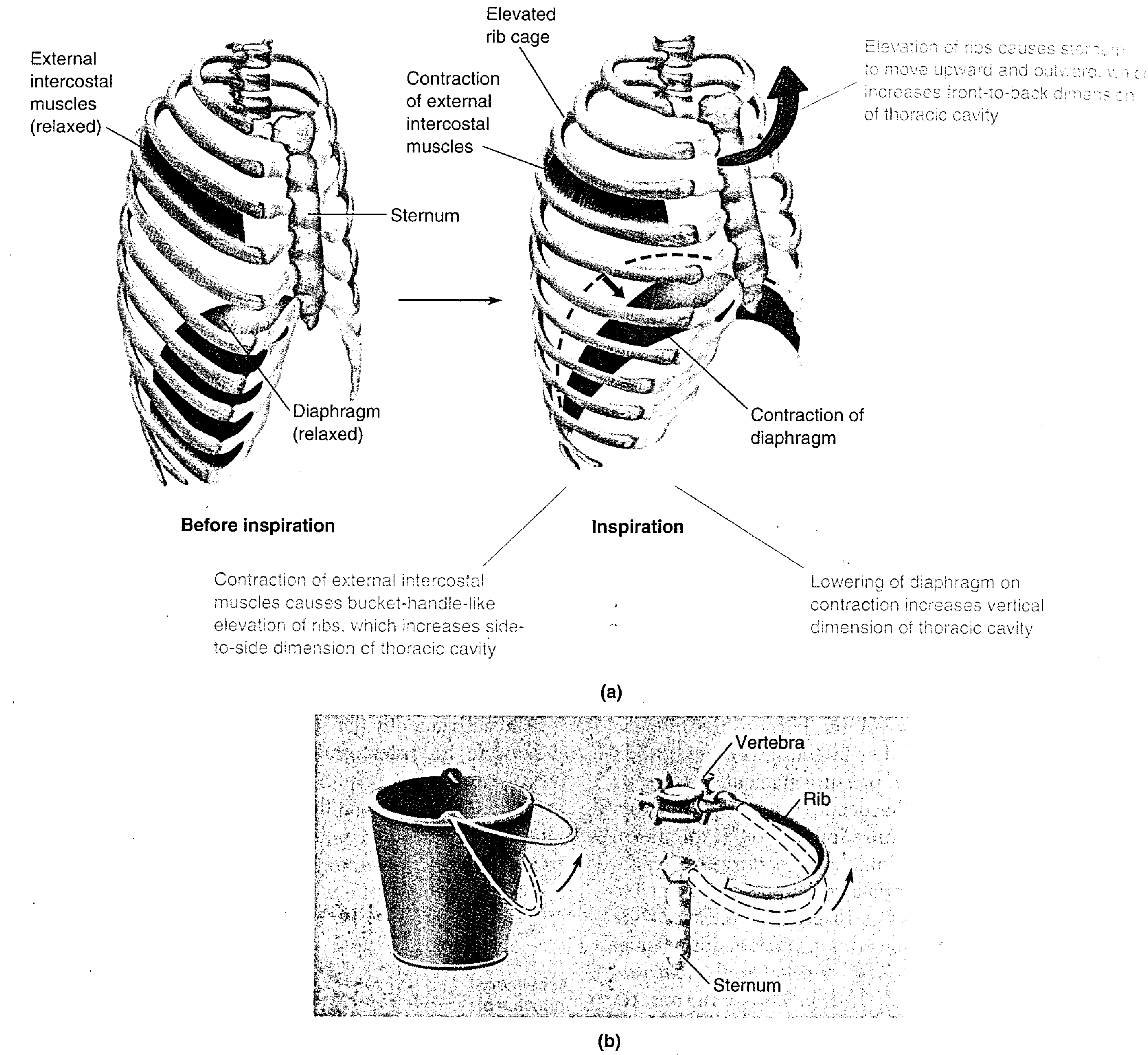


FIGURE 13-11
Anatomy of the respiratory muscles



▌FIGURE 13-12

Respiratory muscle activity during inspiration and expiration

(a) Inspiration, during which the diaphragm descends on contraction, increasing the vertical dimension of the thoracic cavity. Contraction of the external intercostal muscles elevates the ribs and subsequently the sternum to enlarge the thoracic cavity from front-to-back and side-to-side. (b) The rib elevations produced by contraction of the external intercostal muscles are similar to the lifting of a bucket handle. Notice that elevating the bucket handle also moves it *outward*. (c) Quiet passive expiration, during which the diaphragm relaxes, reducing the volume of the thoracic cavity from its peak inspiratory size. As the external intercostal muscles relax, the elevated rib cage falls because of the force of gravity. This also reduces the volume of the thoracic cavity. (d) Active expiration, during which contraction of the abdominal muscles increases the intra-abdominal pressure, exerting an upward force on the diaphragm. This reduces the vertical dimension of the thoracic cavity further than it is reduced during quiet passive expiration. Contraction of the internal intercostal muscles decreases the front-to-back and side-to-side dimensions by flattening the ribs and sternum.

is flowing into or out of the lungs (▌Fig. 13-13a). As the thoracic cavity enlarges, the lungs are also forced to expand to fill the larger thoracic cavity. As the lungs enlarge, the intra-alveolar pressure drops because the same number of air molecules now occupy a larger lung volume. In a typical inspiratory excursion, the intra-alveolar pressure drops 1 mm Hg to 759 mm Hg (Fig. 13-13b). Because the intra-alveolar pressure is now less than atmospheric pressure, air flows into the lungs down the pressure gradient from higher to lower pressure. Air continues to enter the lungs until no further gradient exists—that is, until intra-alveolar pressure equals atmospheric pressure. Thus, lung expansion is not caused by movement of air into the lungs; instead, air flows into the lungs because of the fall in intra-alveolar pressure brought about by lung expansion.

During inspiration, the intrapleural pressure falls to 754 mm Hg as a result of expansion of the thorax. The resultant in-

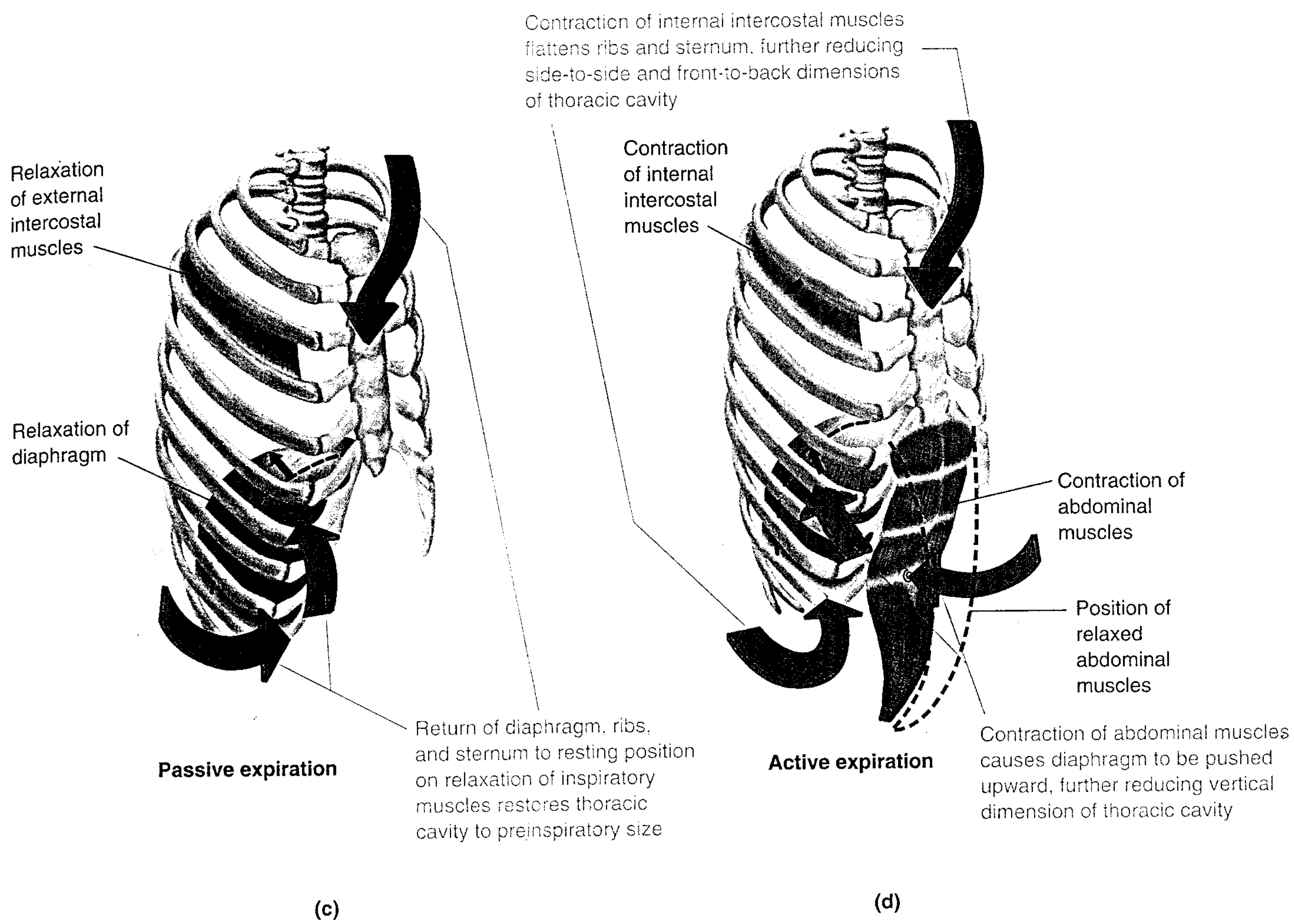


FIGURE 13-12
Respiratory muscle activity during inspiration and expiration (continued)

crease in the transmural pressure gradient during inspiration ensures that the lungs are stretched to fill the expanded thoracic cavity.

Deeper inspirations (more air breathed in) can be accomplished by contracting the diaphragm and external intercostal muscles more forcefully and by bringing the **accessory inspiratory muscles** into play to further enlarge the thoracic cavity. Contraction of these accessory muscles, which are located in the neck (Fig. 13-11 and Table 13-1), raises the sternum and elevates the first two ribs, enlarging the upper portion of the thoracic cavity. As the thoracic cavity increases even further in volume than under resting conditions, the lungs likewise expand even more, dropping the intra-alveolar pressure even further. Consequently, a larger inward flow of air occurs before equilibration with atmospheric pressure is achieved; that is, a deeper breath occurs.

At the end of inspiration, the inspiratory muscles relax. The diaphragm assumes its original dome-shaped position when it relaxes; the elevated rib cage falls because of gravity when the external intercostals relax; and the chest wall and stretched lungs recoil to their preinspiratory size because of their elastic properties, much as a stretched balloon would upon release (Fig. 13-12c). As the lungs recoil and become smaller in volume, the intra-alveolar pressure rises, because the greater number of air molecules contained within the larger lung volume at the end of inspiration are now compressed into a smaller volume. In a resting expiration, the intra-alveolar pressure increases about 1 mm Hg above atmospheric level to 761 mm Hg (Fig. 13-13c). Air now leaves the lungs down its pressure gradient from high intra-alveolar pressure to lower atmospheric pressure. Outward flow of air ceases when intra-alveolar pressure becomes equal to atmospheric pressure and a pressure gradient no longer exists. Figure 13-14 summarizes the intra-alveolar and intrapleural pressure changes that take place during one respiratory cycle.

During quiet breathing, expiration is normally a *passive* process, since it is accomplished by elastic recoil of the lungs on relaxation of the inspiratory muscles, with no muscular exertion or energy expenditure required. In contrast, inspiration is *always active*, because it is brought about only by contraction of inspiratory muscles at the expense of energy utilization. To empty the lungs more completely and more rapidly than is accomplished during quiet breathing, as during the deeper breaths accompanying exercise, expiration does become active. The intra-alveolar pressure must be increased even further above atmospheric pressure than can be accomplished by simple relaxation of the inspiratory muscles and elastic recoil of the lungs. To produce such a **forced, or active, expiration, expiratory muscles** must contract to further reduce the volume of the thoracic cavity and lungs (Figs. 13-11 and 13-12