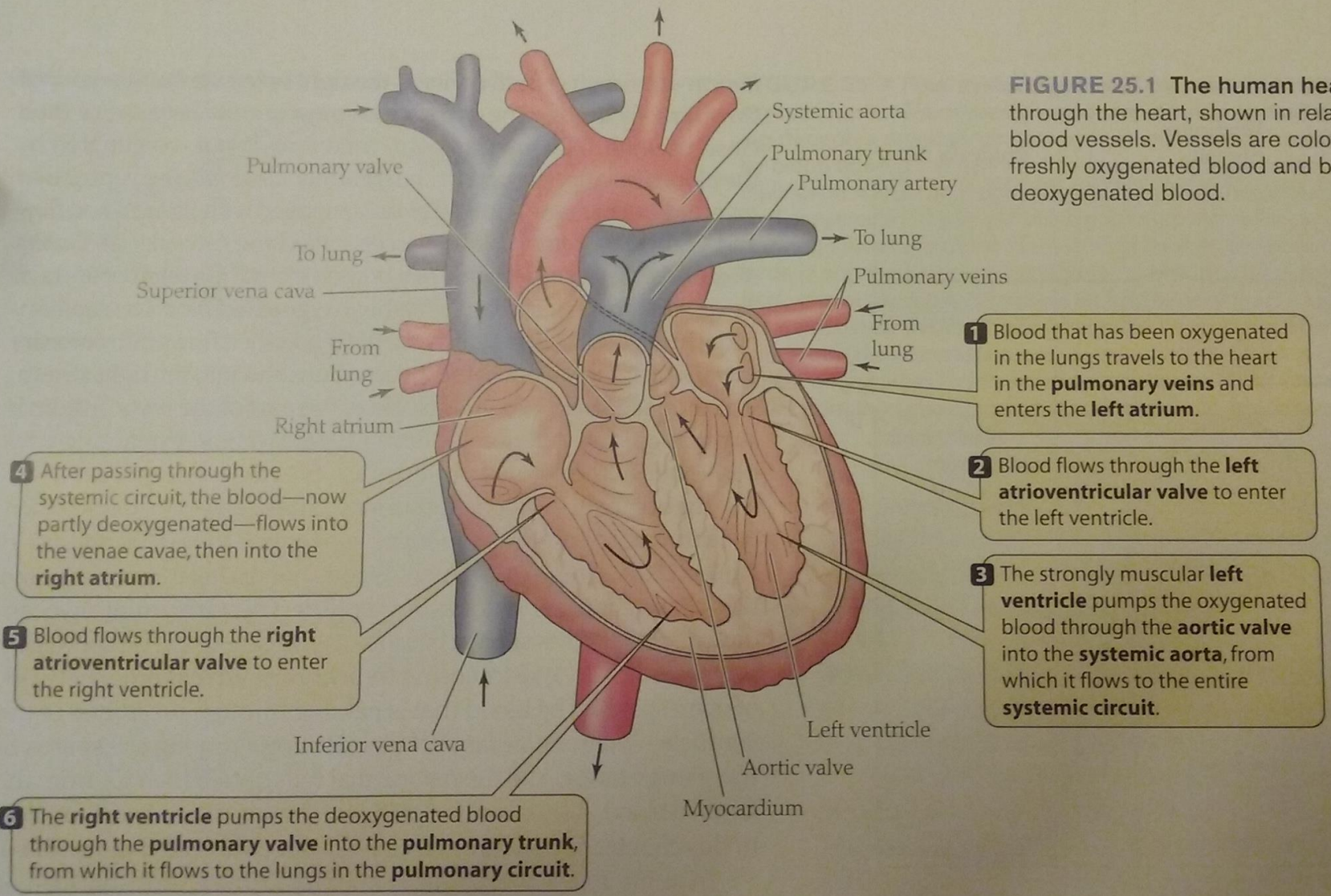
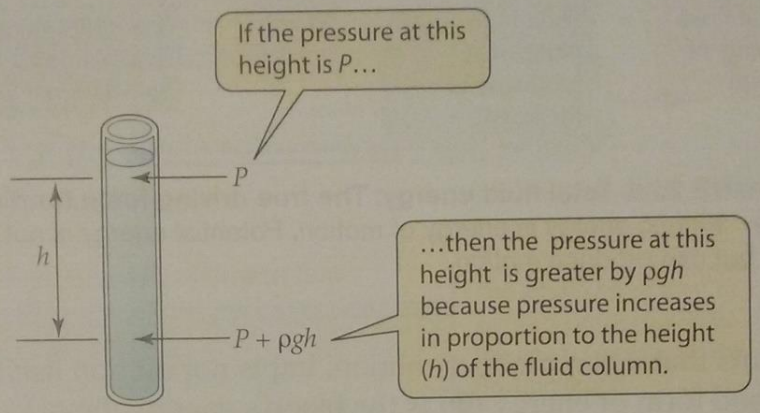


FIGURE 25.1 The human heart A section through the heart, shown in relation to the attached blood vessels. Vessels are colored red if they carry freshly oxygenated blood and blue if they carry partly deoxygenated blood.

(*a*) The physics of fluid-column effects in an unobstructed vertical tube



(*b*) Mean blood pressure in major arteries of a quietly standing person

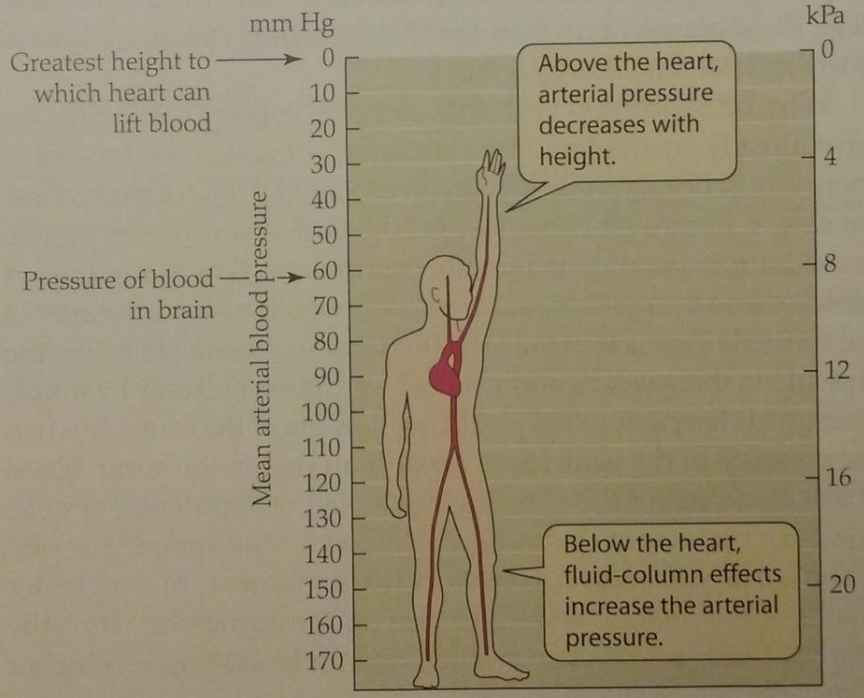


FIGURE 25.7 Fluid-column effects on blood pressure in the arterial vascular system (*a*) The physics of fluid-column effects in an unobstructed, vertically positioned tube filled with a nonmoving fluid. The symbol *h* represents the difference in height between two points within the fluid column, ρ is the mass density of the fluid, and *g* is acceleration due to gravity. (*b*) Fluid-column effects on arterial blood pressure in a person standing quietly. (*b* after Rushmer 1976.)

analyzed using the pressure developed by the heart as the sole driving force.[14] This is the approach we will use except in special cases.

The rate of blood flow depends on differences in blood pressure and on vascular resistance

Already in the nineteenth century, physiologists were seeking to understand the perfusion of blood vessels by analyzing the steady, nonturbulent flow of a simple liquid such as water through a horizontal, rigid-walled tube (Figure 25.9*a*). Their analyses led to insights that are still considered important today. The factors that determine the rate of flow (mL/minute) from one end of a tube to the other, they discovered, are the pressure at the entry to the tube (P_{in}), the pressure at the exit (P_{out}), the radius of the lumen of the tube (r), the tube length (l), and the viscosity of the liquid (η).[15] The formula relating these quantities is named the **Poiseuille equation** or **Hagen–Poiseuille equation**, after Jean Poiseuille (1797–1869) and Gotthilf Hagen (1797–1884), who derived it:

$$\text{Flow rate} = (P_{in} - P_{out})\left(\frac{\pi}{8}\right)\left(\frac{1}{\eta}\right)\left(\frac{r^4}{l}\right) \qquad (25.2)$$

rigid-walled tubes. Blood is not a simple liquid because it contains suspended cells, and blood vessels are not unbranched or rigid-walled. Nonetheless, the Poiseuille equation often proves to be a useful approximate model for understanding the flow of blood through blood vessels. From the Poiseuille equation, we see that *when muscles in the walls of a blood vessel change the radius of the vessel by contracting or relaxing, they exert profound (fourth power) control over the rate of flow through the vessel.*

Another equation that is useful for understanding the rate of steady blood flow through a horizontal system of blood vessels is

$$\text{Flow rate} = \frac{\Delta P}{R} \qquad \textbf{(25.3)}$$

where ΔP is the difference in blood pressure between the entry vessels of the vascular system and the exit vessels, and R is the resistance to flow through the system, termed the **vascular resistance**. This equation (analogous to Ohm's law in electrical circuits) simply says that the rate of flow increases when the difference in pressure increases, but the rate of flow decreases when the vascular resistance increases. If we consider a simple tubular vessel, an easy relation exists between Equation 25.3 and the Poiseuille equation. Because ΔP and $(P_{in} - P_{out})$ represent the same quantity in this case, the resistance R is equal to $8\eta l/\pi r^4$. One can see that *resistance is inversely proportional to the fourth power of the vessel radius.* Halving the radius of a vessel increases the resistance to flow through the vessel by a factor of 16.

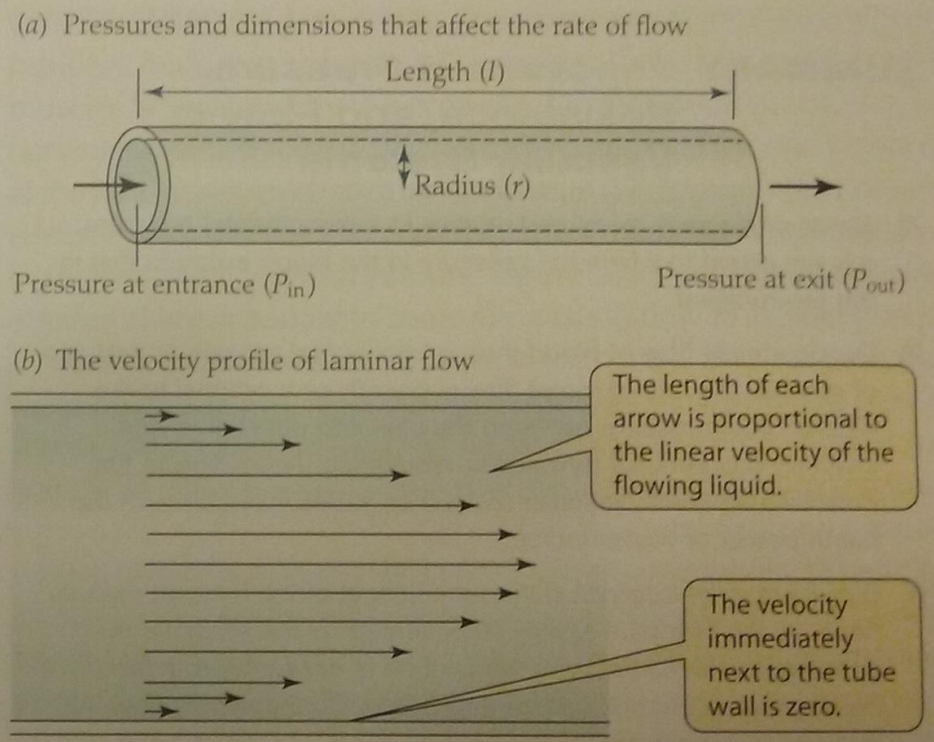


FIGURE 25.9 The physics of flow through tubes (*a*) Critical factors for understanding the rate of flow using the Poiseuille equation. (*b*) Linear velocity as a function of distance from the tube wall. A microscopically thin layer of liquid touching the tube wall does not move at all. The velocity profile seen here applies when a simple liquid such as water flows in a laminar fashion through a tube; the velocity profile for blood differs from that for a simple liquid.

SUMMARY Principles of Pressure, Resistance, and Flow in Vascular Systems

- Blood pressure is measured relative to environmental pressure; it is the extent to which the pressure in the blood exceeds that in the environment.
- During steady flow of blood through horizontal vessels or systems of vessels, the rate of blood flow is directly proportional to the difference of pressure between the inlet and outlet. It is also inversely proportional to vascular resistance. According to the Poiseuille equation, vascular resistance varies inversely with the fourth power of vessel radius.
- Blood pressure declines during the flow of blood through vessels because the potential energy represented by the pressure is converted to kinetic energy, which then is converted to heat in overcoming viscous resistance to flow. During steady flow through a horizontal system, this drop in blood pressure is a measure of the energy cost of perfusion.

peripheral parts of the circulatory system. The elasticity of the great arteries enables them to perform important hydrodynamic functions. If the heart were to discharge blood into rigid, inelastic tubes, the blood pressure would oscillate violently upward and downward with each contraction and relaxation of the heart. Instead, the arteries are elastic. They stretch when they receive blood discharged from the heart. Some of

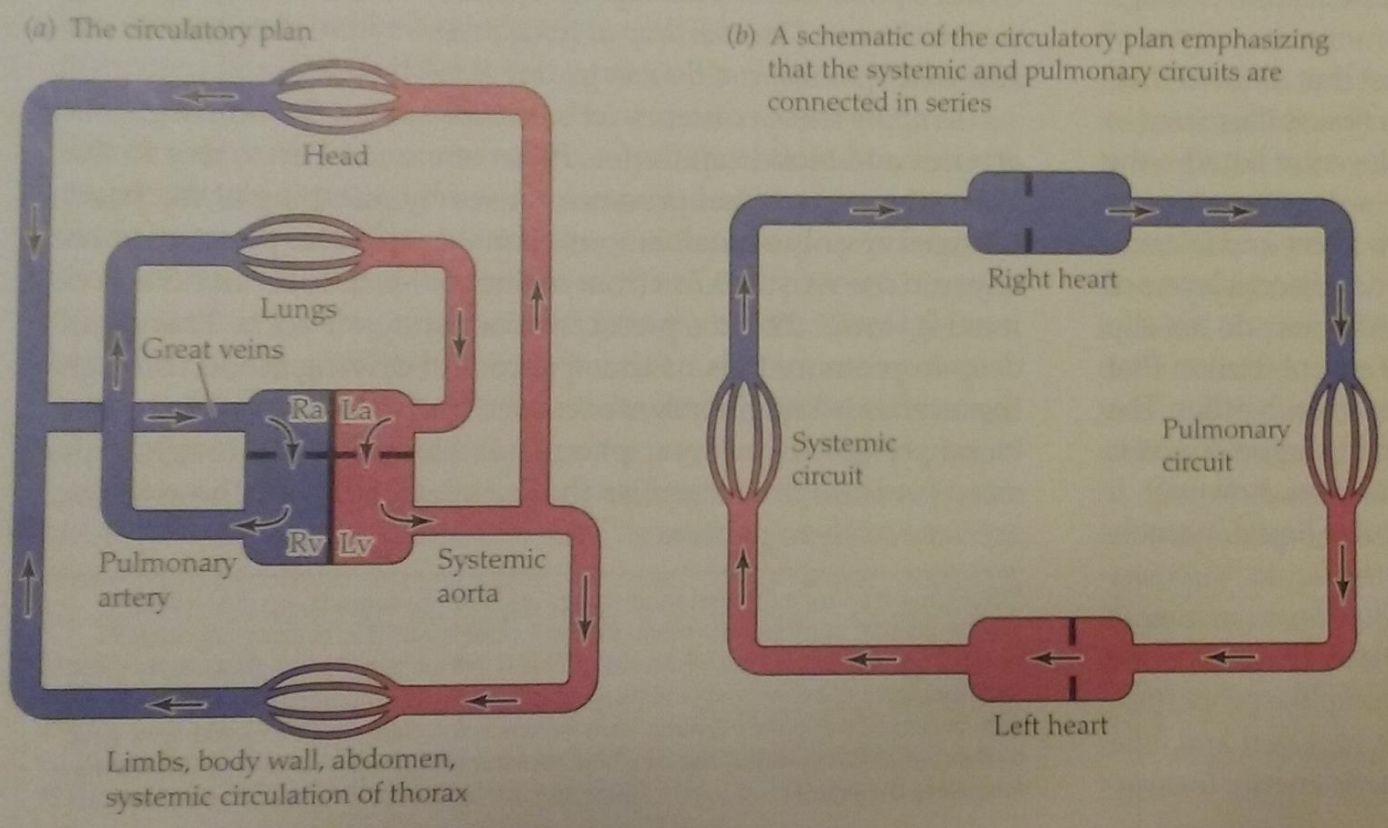


FIGURE 25.10 The circulatory plan in mammals and birds (*a*) The circulatory plan as it exists geometrically in the body. (*b*) The same plan, redrawn as a schematic to emphasize the arrangement of the pulmonary and systemic circuits in series with each other. Red and blue portions carry relatively oxygenated and deoxygenated blood, respectively. Ra, right atrium of the heart; La, left atrium; Rv, right ventricle; Lv, left ventricle.

TABLE 25.1 Systolic and diastolic blood pressures in the arteries leaving the heart and the cardiac outputs of some resting vertebrates[a]

Species	Blood pressure (mm Hg)[b]		Cardiac output (mL/kg·min)
	Systolic	Diastolic	
Human (young adult male)	120	75	80–90
Bottlenose dolphin	150	121	47–105
Horse	171	103	150
Ground squirrel	139	99	313
Laboratory rat	130	91	209
Bobwhite quail	147	132	—
Pekin duck	181	134	—
Sparrow	180	140	—
Turtle	25	10	57
Iguana	48	37	58
Leopard frog	32	21	20–30
Rainbow trout	45	33	18–37
Catfish	40	30	11
Dogfish shark	30	24	25

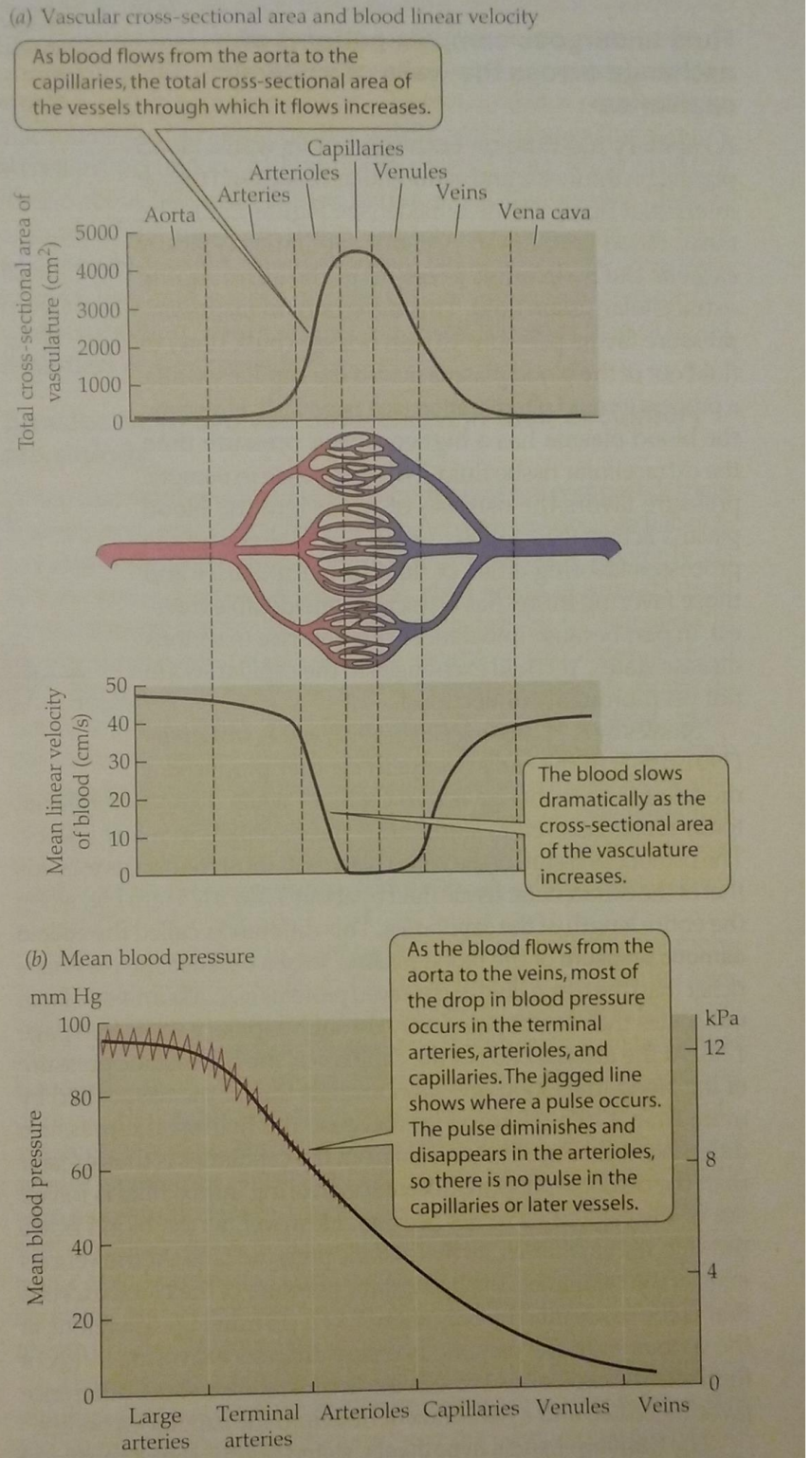


FIGURE 25.12 Blood flow in the human systemic vasculature
(*a*) Cross-sectional area and linear velocity of blood flow in the various parts of the systemic vasculature. Although the cross-sectional area

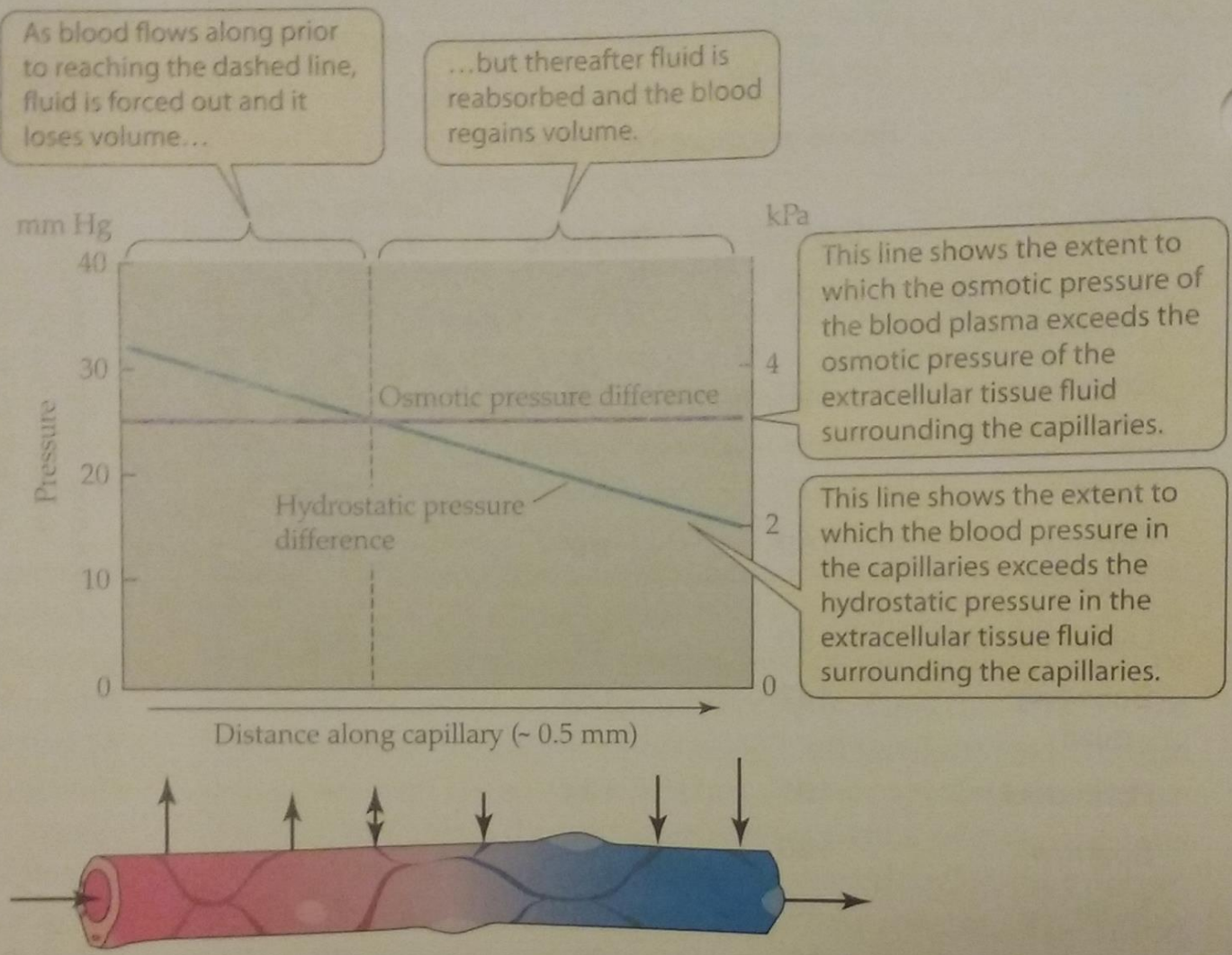


FIGURE 25.13 Fluid exchange across mammalian systemic capillary walls: The Starling–Landis hypothesis The walls of blood capillaries are *fenestrated* in most tissues, meaning that they are densely perforated by minute physical pores such as gaps between adjacent cells (see page 701). Ultrafiltration occurs readily through these fenestrations. Osmosis of water occurs readily because of the thinness of the endothelial cells, fenestrations, and presence of aquaporins in the cell membranes. The image of the capillary at the bottom shows the direction of net fluid exchange. On the graph, the osmotic-pressure difference can be represented as a horizontal line because the losses and gains of fluid volume are not great enough to change the relative osmotic pressures substantially. Values are approximate.

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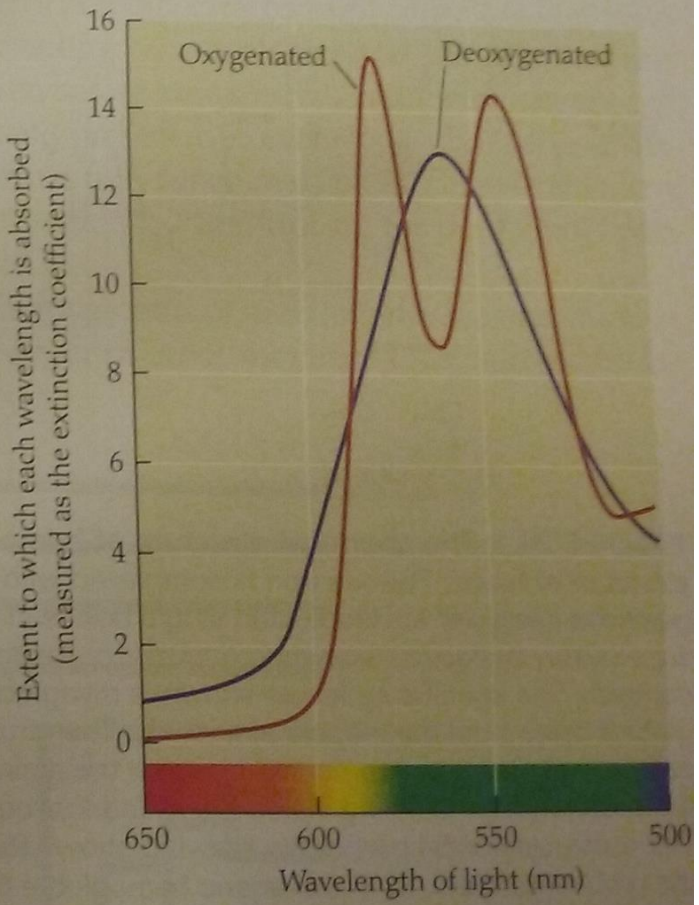
SUMMARY Circulation in Mammals and Birds

- Mammals and birds, like virtually all other vertebrates, have closed circulatory systems, meaning that the blood always remains within blood vessels lined with vascular endothelium.
- The pulmonary and systemic circuits are connected in series. The left ventricle develops high pressures to force blood through the high-resistance systemic circuit. The right ventricle develops lower pressures to force blood through the low-resistance pulmonary circuit.
- In the systemic circuit, arteries convey blood over relatively long distances with little loss of blood pressure; arteries also perform pressure-damping and pressure-reservoir functions because of their elasticity. Arterioles in the systemic microcirculatory beds exert fine spatial and temporal control over blood flow by contraction and relaxation of the smooth muscles in their walls (vasomotor controls). The capillaries are the principal sites of exchange between the blood and systemic tissues because their walls consist of just a single layer of fenestrated endothelial cells rich in aquaporins and because they are densely distributed.
- As blood flows through systemic capillaries, blood pressure tends to force fluid to pass outward through the capillary walls by ultrafiltration. The colloid osmotic pressure of the blood plasma tends to cause fluid movement into the blood. The net effect of this interplay is a loss of fluid, which is picked up by the lymphatic system. The lower blood pressures in the pulmonary circuit help to prevent pulmonary flooding (edema).
- During exercise, cardiac output is augmented by increases in both heart rate and stroke volume. Arterial blood pressure does not rise excessively because vascular resistance is decreased, mainly by vasodilation in active muscles.

BOX 24.1 ABSORPTION SPECTRA OF RESPIRATORY PIGMENTS

The hemoglobins and other respiratory pigments—like all pigments—differentially absorb various wavelengths of light. The pattern of absorption by a pigment when expressed as a function of wavelength, is known as an **absorption spectrum** (plural *spectra*). The absorption spectrum of a specific respiratory pigment (e.g., human hemoglobin) changes with the oxygenation or deoxygenation of the pigment, as shown in the accompanying figure. These changes are qualitatively evident to our eyes: We know, for example, that oxygenated hemoglobin (bright red) differs in color from deoxygenated hemoglobin (purple-red). By using quantitative light-absorption measurements, the percentage of heme groups that are oxygenated in blood can be determined. This is the principle behind the finger probes—known as *pulse oximeters*—that are used to monitor arterial blood oxygenation in hospital patients. **Box Extension 24.1** explains how a pulse oximeter measures the percentage of oxygenated heme groups in arterial blood and why it is called a "pulse" oximeter.

Absorption spectra for fully oxygenated and fully deoxygenated human hemoglobin To measure absorption, light of each wavelength is passed through a hemoglobin solution of defined concentration and optical path length (in the case shown here, the concentration was 1 m*M*, and the light path through the solution was 1 cm long). The fraction of the incoming photon energy that fails to pass through the solution is measured. From the data, one calculates the *extinction coefficient*, which is a measure of the absorption of the light by the hemoglobin: A high extinction coefficient signifies high absorption. (After Waterman 1978.)



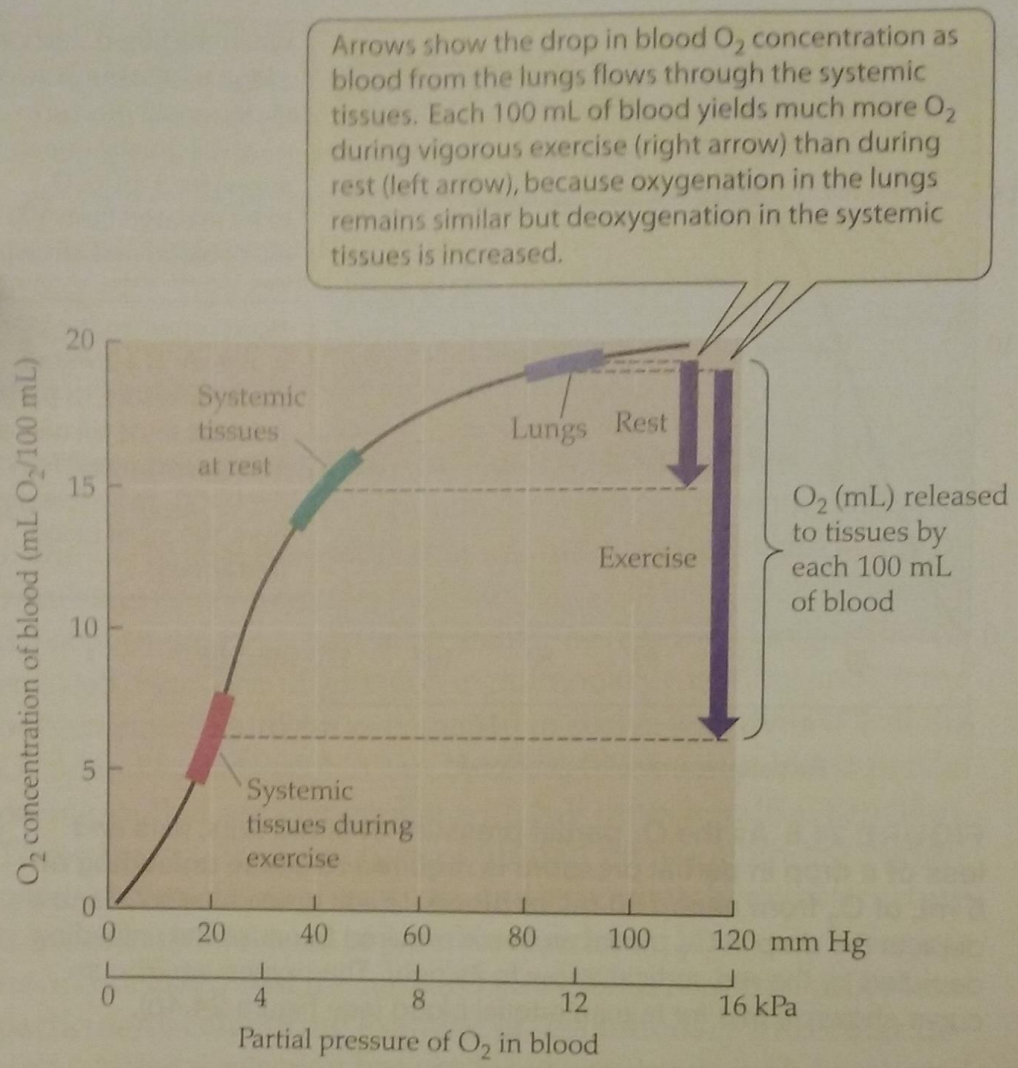


FIGURE 24.5 Oxygen delivery by human blood at rest and during vigorous exercise The oxygen equilibrium curve shown is that for human arterial blood (see Figure 24.4*b*). The thickened, shaded areas on the curve show representative ranges of blood O_2 concentration and O_2 partial pressure in the lungs (blue), the systemic tissues during rest (green), and the systemic tissues during vigorous exercise (red). The vertical purple arrows to the right show how much O_2 is delivered to the tissues by each 100 mL of blood during rest and exercise. All values are semi-quantitative; the intent of this diagram is conceptual rather than literal. Tissue values are mixed venous blood values. Effects of pH and other variables of the blood-hemoglobin milieu are not included.

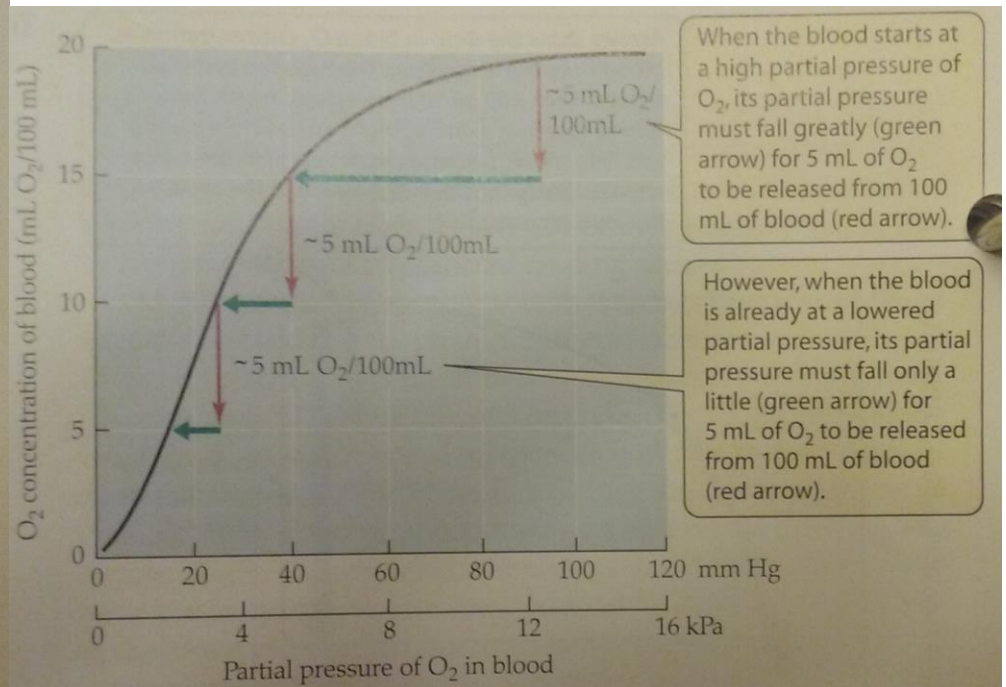


FIGURE 24.6 As the O_2 partial pressure of blood falls, less and less of a drop in partial pressure is required to cause unloading of 5 mL of O_2 from each 100 mL of blood Each green horizontal arrow depicts the drop in O_2 partial pressure required to cause the unloading depicted by the red vertical arrow to its right. The oxygen equilibrium curve shown is that for human arterial blood (see Figure 24.4*b*).

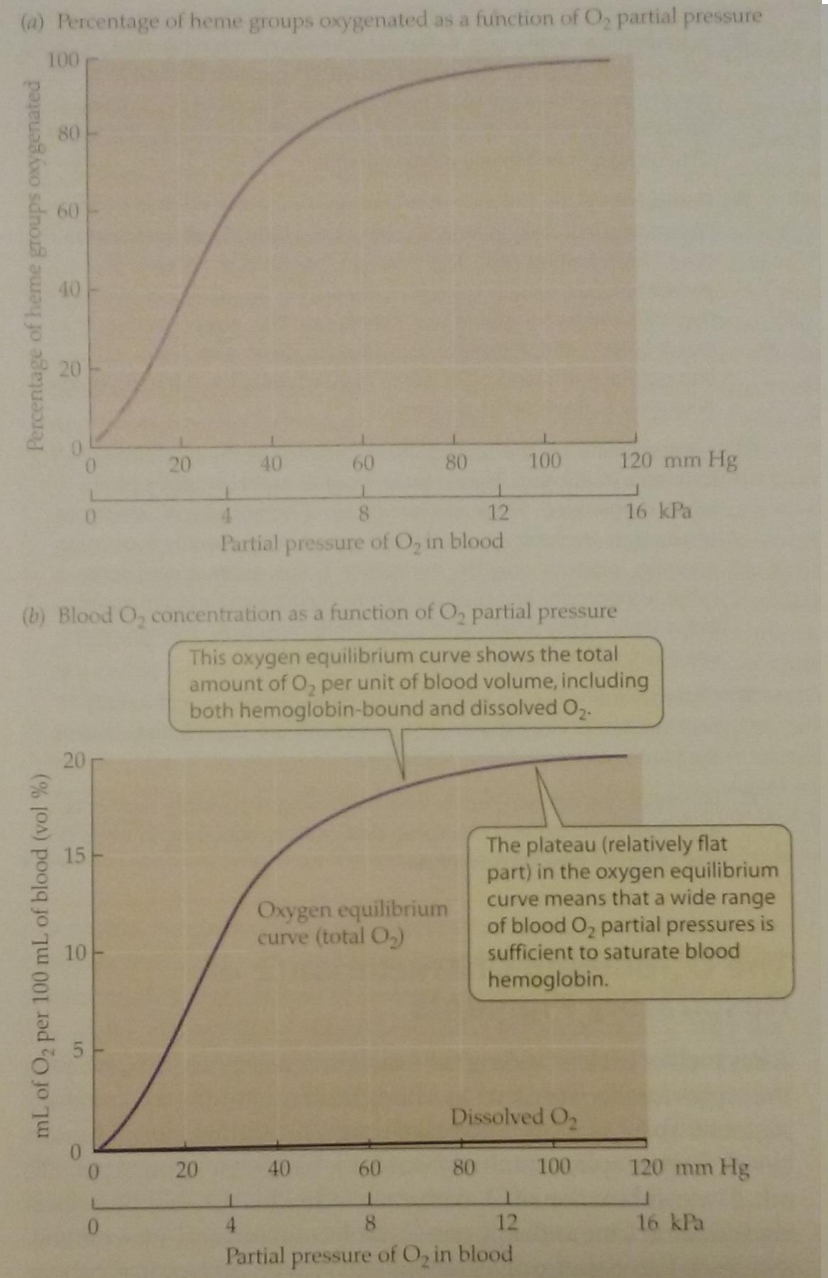


FIGURE 24.4 A typical oxygen equilibrium curve for human arterial blood presented in two different ways (*a*) The percentage of heme groups oxygenated as a function of the O_2 partial pressure. (*b*) The total blood O_2 concentration—including both hemoglobin-bound and dissolved O_2—as a function of the O_2 partial pressure; the portion of the total O_2 present as dissolved O_2 is plotted at the bottom. Normal arterial values of CO_2 partial pressure, pH, and temperature are assumed. In humans, as in other animals, significant individual variation occurs. (After Roughton 1964; *b* assumes an O_2 concentration of 20 vol % at 16 kPa.)

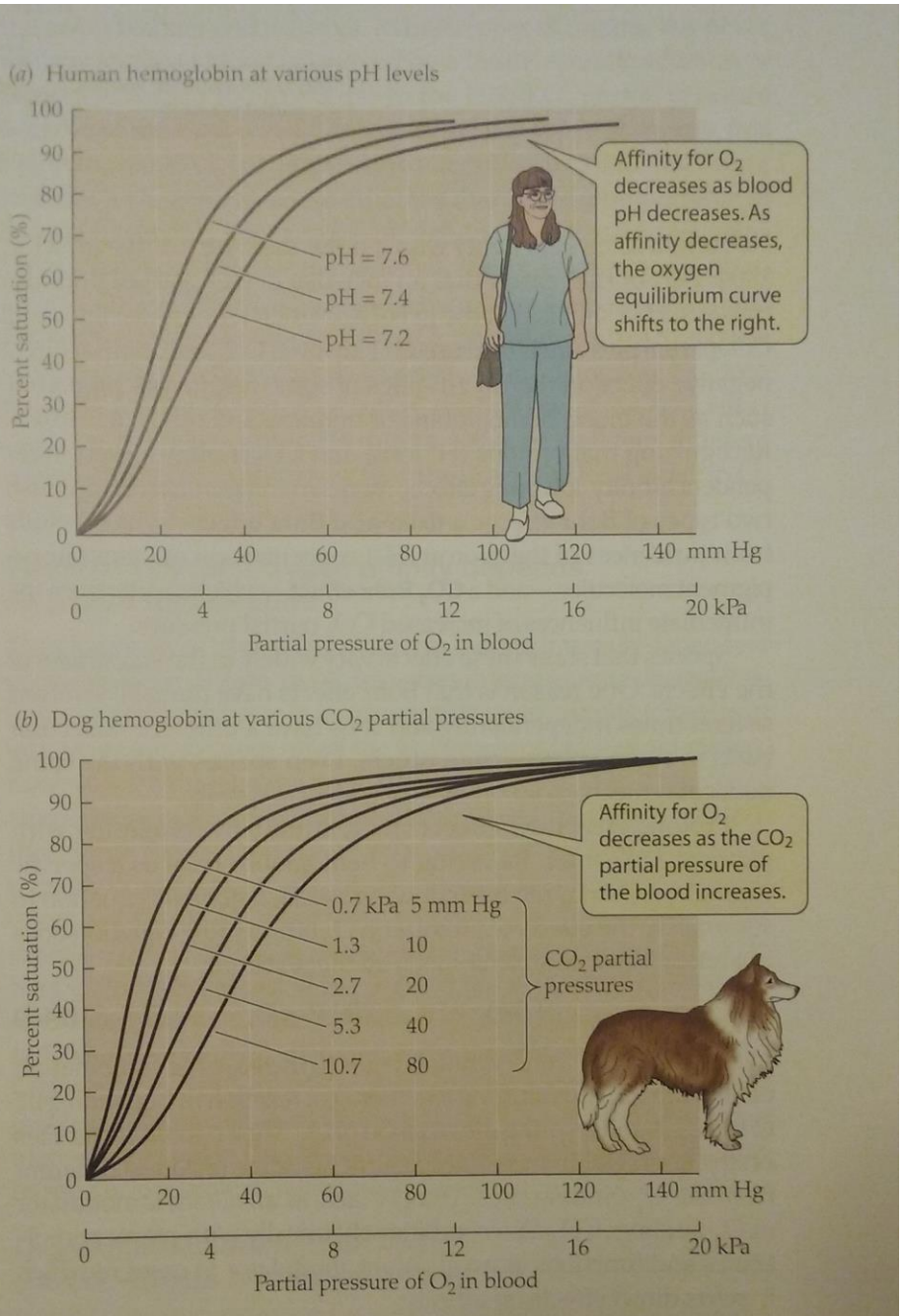


FIGURE 24.11 The Bohr effect: Affinity for O_2 decreases as pH decreases or CO_2 partial pressure increases (*a*) Oxygen equilibrium curves of human hemoglobin at three different pHs at 38°C. In resting humans, the normal pH of arterial blood is about 7.4, whereas that of mixed venous blood is about 0.04 unit less. (*b*) Oxygen equilibrium curves of dog hemoglobin at five different CO_2 partial pressures at 38°C. The data in part (*b*) are from the original work of Bohr and his coworkers. (After Roughton 1964.)