CHAPTER 12

An Overview of the Circulation and Hemodynamics

Thom W. Rooke, M.D.
Harvey V. Sparks, Jr., M.D.

CHAPTER OUTLINE

- ONCE AROUND THE CIRCULATION
- HEMODYNAMIC PRINCIPLES OF THE CARDIOVASCULAR SYSTEM
- PRESSURES IN THE CARDIOVASCULAR SYSTEM
- SYSTOLIC AND DIASTOLIC PRESSURES
- TRANSPORT IN THE CARDIOVASCULAR SYSTEM
- THE LYMPHATIC CIRCULATION
- CONTROL OF THE CIRCULATION

KEY CONCEPTS

1. The circulatory system contributes to the maintenance of the internal environment by transporting nutrients to and waste products away from individual cells of the body. It also participates in the maintenance of the electrolyte and thermal environment of cells.
2. The circulatory system consists of two pumps in series. The right heart pumps blood into the lungs. The left heart pumps blood through the rest of the body.
3. The transport of nutrients and wastes over long distances (along the length of the blood vessels) occurs by bulk flow whereas transport over short distances (across the capillary walls) occurs via diffusion.
4. Pressure, flow, and resistance are related by Ohm's law.
5. Poiseuille's law shows how the radius and length of a vessel and blood viscosity contribute to vascular resistance.
6. The contractions of the heart generate the pressure that drives blood through the pulmonary and systemic circulations.

The physiological and medical importance of the cardiovascular system has been apparent since William Harvey first described the circulation of blood in 1628. A properly functioning, well-regulated cardiovascular system is essential to the maintenance of the internal environment of the body. Each cell must receive oxygen from the lungs and a variety of nutrients from the gastrointestinal tract. Each cell produces waste products that must be removed from its environment and taken to the lungs, kidneys, or other organs for metabolism and/or excretion. Cells in endocrine glands communicate with cells in other tissues by releasing hormones that are carried throughout the body by the circulation. Heat produced by the work of the body is brought to the surface of the body where it can be lost to the external environment by way of the circulation.

The circulatory system must perform all of these functions in the face of a variety of challenges, such as exercise, hot and cold environments, changes in posture, pregnancy and childbirth, and the hypoxia caused by high altitudes. Unfortunately, failure of the cardiovascular system to perform normally occurs all too often. In developed countries, the leading causes of death and morbidity include myocardial infarction, stroke, hypertension, congestive heart failure, and an assortment of other cardiovascular problems. Knowledge of the structure and function of the cardiovascular system is, therefore, crucial for understanding many aspects of health and disease.

ONCE AROUND THE CIRCULATION

An understanding of the circulation depends on knowledge of the physical principles governing blood flow. But first, we will briefly describe the cardiovascular system (Fig. 12.1). Contractions of the left ventricle propel blood into the aorta, the large arteries, and the vasculature beyond. Because of their elasticity, the aorta and large arteries are distended by each injection of blood from the heart. The aorta and large arteries recoil between ventricular contractions, continuing the flow of blood to the periphery.

Several regulatory mechanisms normally keep aortic pressure within a narrow range, providing a pulsatile but

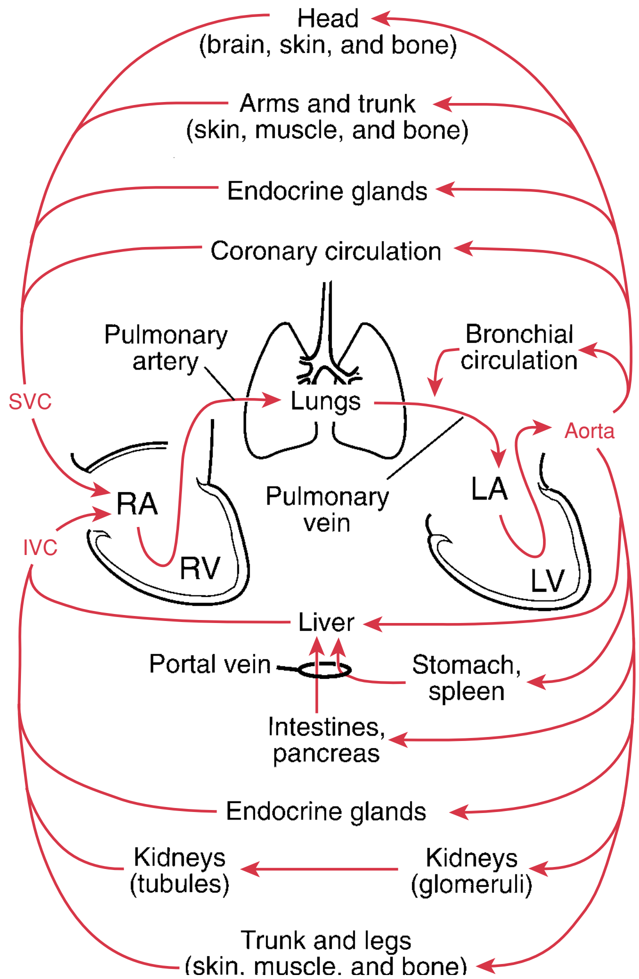


FIGURE 12.1 **A model of the cardiovascular system.** The right and left hearts are aligned in series, as are the systemic circulation and the pulmonary circulation. In contrast, the circulations of the organs other than the lungs are in parallel; that is, each organ receives blood from the aorta and returns it to the vena cava. Exceptions are the various "portal" circulations, which include the liver, kidney tubules, and hypothalamus. SVC, superior vena cava; IVC, inferior vena cava; RA, right atrium; RV, right ventricle; LA, left atrium; LV, left ventricle.

consistent pressure and driving blood to the small arteries and arterioles. Smooth muscle in the relatively thick walls of small arteries and arterioles can contract or relax, causing large changes in flow to a particular organ or tissue. Because of their ability to adjust their caliber, small arteries and arterioles are called **resistance vessels**. The prominent pressure pulsations in the aorta and large arteries are damped by the small arteries and arterioles. Pressure and flow are steady in the smallest arterioles.

Blood flows from arterioles into the capillaries. Capillaries are small enough that red blood cells flow through them in single file. They are numerous enough so that every cell in the body is close enough to a capillary to receive the nutrients it needs. The thin capillary walls allow rapid exchanges of oxygen, carbon dioxide, substrates, hormones, and other molecules and, for this reason, are called **exchange vessels**.

Blood flows from capillaries into venules and small veins. These vessels have larger diameters and thinner walls than the companion arterioles and small arteries. Because of their larger caliber they hold a larger volume of blood. When the smooth muscle in their walls contracts, the volume of blood they contain is reduced. These vessels, along with larger veins, are referred to as **capacitance vessels**. The pressure generated by the contractions of the left ventricle is largely dissipated by this point; blood flows through the veins to the right atrium at much lower pressures than are found on the arterial side of the circulation.

The right atrium receives blood from the largest veins, the superior and inferior vena cavae, which drain the entire body except the heart and lungs. The thin wall of the right atrium allows it to stretch easily to store the steady flow of blood from the periphery. Because the right ventricle can receive blood only when it is relaxing, this storage function of the right atrium is critical. The muscle in the wall of the right atrium contracts at just the right time to help fill the right ventricle. Contractions of the right ventricle propel blood through the lungs where oxygen and carbon dioxide are exchanged in the pulmonary capillaries. Pressures are much lower in the **pulmonary circulation** than in the **systemic circulation**. Blood then flows via the pulmonary vein to the left atrium, which functions much like the right atrium. The thick muscular wall of the left ventricle develops the high pressure necessary to drive blood around the systemic circulation.

The mechanisms that regulate all of the above anatomic elements of the circulation are the subject of the next few chapters. In this chapter, we consider the physical principles on which the study of the circulation is based.

HEMODYNAMIC PRINCIPLES OF THE CARDIOVASCULAR SYSTEM

Hemodynamics is the branch of physiology concerned with the physical principles governing pressure, flow, resistance, volume, and compliance as they relate to the cardiovascular system. These principles are used in the next few chapters to explain the performance of each part of the cardiovascular system.

Poiseuille's Law Describes the Relationship Between Pressure and Flow

Fluid flows when a pressure gradient exists. **Pressure** is force applied over a surface, such as the force applied to the cross-sectional surface of a fluid at each end of a rigid tube. The height of a column of fluid is often used as a measure of pressure. For example, the pressure at the bottom of a container containing a column of water 100 cm high is 100 cm of H_2O. The height of a column of mercury (Fig. 12.2) is frequently used for this purpose because it is dense (approximately 13 times more dense than water), and a relatively small column height can be used to measure physiological pressures. For example, mean arterial pressure is equal to the pressure at the bottom of a column of mercury approximately 93 mm high (abbreviated 93 mm Hg). If the same arterial pressure were measured

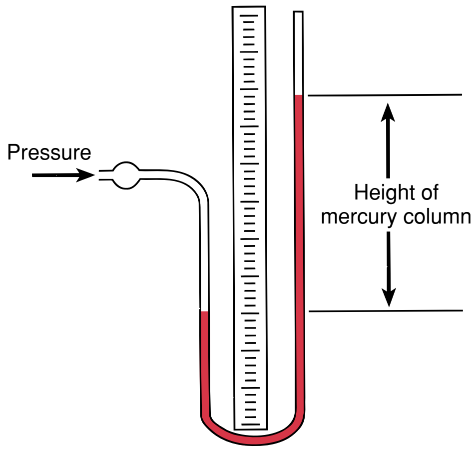


FIGURE 12.2 **Pressure expressed as the height of a column of fluid.** For the measurement of arterial pressures it is convenient to use mercury instead of water because its density allows the use of a relatively short column. A variety of electronic and mechanical transducers are used to measure blood pressure, but the convention of expressing pressure in mm Hg persists.

using a column of water, the column would be approximately 4 ft (or 1.3 m) high.

The **flow** of fluid through rigid tubes is governed by the pressure gradient and resistance to flow. Resistance depends on the radius and length of the tube as well as the viscosity of the fluid. All of this is summarized by **Poiseuille's law**. While not exactly descriptive of blood flow through elastic, tapering blood vessels, Poiseuille's law is useful in understanding blood flow. The volume of fluid flowing through a rigid tube per unit time (**Q**) is proportional to the pressure difference (ΔP) between the ends of the tube and inversely proportional to the **resistance to flow** (R):

$$Q = \Delta P/R \quad (1)$$

When fluid flows through a tube, the resistance to flow (R) is determined by the properties of both the fluid and the tube. Poiseuille found that the following factors determine resistance to steady, streamlined flow of fluid through a rigid, cylindrical tube:

$$R = 8\eta L/\pi r^4 \quad (2)$$

where r is the radius of the tube, L is its length, and η is the viscosity of the fluid; 8 and π are geometrical constants. Equation 2 shows that the resistance to blood flow increases proportionately with increases in fluid viscosity or tube length. In contrast, radius changes have a much greater influence because resistance is inversely proportional to the fourth power of the radius (Fig. 12.3). Equation 1 shows that if pressure and flow are expressed in units of mm Hg and mL/min, respectively, R is in mm Hg /(mL/min). The term **peripheral resistance unit** (PRU) is often used instead.

Poiseuille's law incorporates all of the factors influencing flow, so that

$$Q = \Delta P \pi r^4/8\eta L \quad (3)$$

In the body, changes in radius are usually responsible for variations in blood flow. Length does not change. Although blood viscosity increases with hematocrit and with plasma protein concentration, blood viscosity only rarely changes enough to have a significant effect on resistance. Numerous control systems exist for the sole purpose of maintaining the arterial pressure relatively constant so there is a steady force to drive blood through the cardiovascular system. Small changes in arteriolar radius can cause large changes in flow to a tissue or organ because flow is related to the fourth power of the radius.

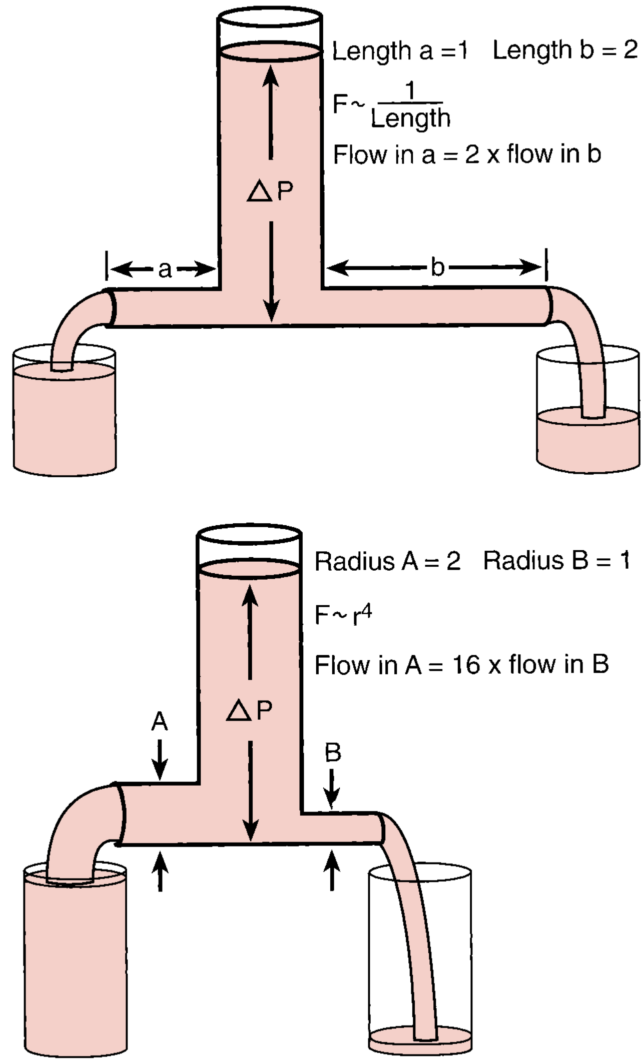


FIGURE 12.3 **The influence of tube length and radius on flow.** Because flow is determined by the fourth power of the radius, small changes in radius have a much greater effect than small changes in length. Furthermore, changes in blood vessel length do not occur over short periods of time and are not involved in the physiological control of blood flow. The pressure difference (ΔP) driving flow is the result of the height of the column of fluid above the openings of tubes A and B.

Conditions in the Cardiovascular System Deviate From the Assumptions of Poiseuille's Law

Despite the usefulness of Poiseuille's law, it is worthwhile to examine the ways the cardiovascular system does not strictly meet the criteria necessary to apply the law. First, the cardiovascular system is composed of tapering, branching, elastic tubes, rather than rigid tubes of constant diameter. These conditions, however, cause only small deviations from Poiseuille's law.

Application of Poiseuille's law requires that flow be steady rather than pulsatile, yet the contractions of the heart cause cyclical alterations in both pressure and flow. Despite this, Poiseuille's law gives a good estimate of the relationship between pressure and flow averaged over time.

Another criterion for applying Poiseuille's law is that flow be streamlined. **Streamline (laminar) flow** describes the movement of fluid through a tube in concentric layers that slip past each other. The layers at the center have the fastest velocity and those at the edge of the tube have the slowest. This is the most efficient pattern of flow velocities, in that the fluid exerts the least resistance to flow in this configuration. **Turbulent flow** has crosscurrents and eddies, and the fastest velocities are not necessarily in the middle of the stream. Several factors contribute to the tendency for turbulence: high flow velocity, large tube diameter, high fluid density, and low viscosity. All of these factors can be combined to calculate **Reynolds number** (N_R), which quantifies the tendency for turbulence:

$$N_R = v d \rho / \eta \quad (4)$$

where v is the mean velocity, d is the tube diameter, ρ is the fluid density, and η is the fluid viscosity. Turbulent flow occurs when N_R exceeds a critical value. This value is hardly ever exceeded in a normal cardiovascular system, but high flow velocity is the most common cause of turbulence in pathological states.

Figure 12.4 shows that the relationship between pressure gradient along a tube and flow changes at the point that streamline flow breaks into eddies and crosscurrents (i.e., turbulent flow). Once turbulence occurs, a given increase in pressure gradient causes less increase in flow because the turbulence dissipates energy that would otherwise drive flow. Under normal circumstances, turbulent flow is found only in the aorta (just beyond the aortic valve) and in certain localized areas of the peripheral system, such as the carotid sinus. Pathological changes in the cardiac valves or a narrowing of arteries that raise flow velocity often induce turbulent flow. Turbulent flow generates vibrations that are transmitted to the surface of the body; these vibrations, known as **murmurs** and **bruits**, can be heard with a stethoscope.

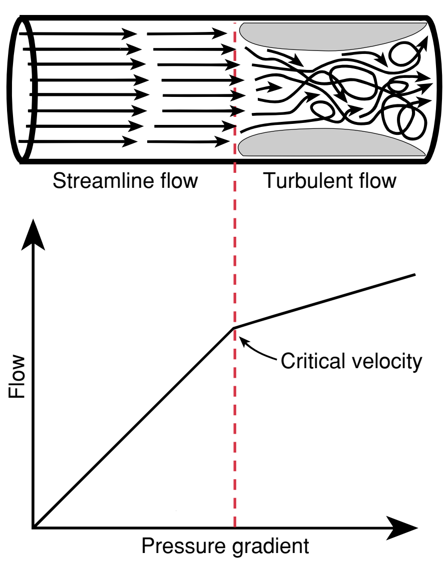


FIGURE 12.4 **Streamline and turbulent blood flow.** Blood flow is streamlined until a critical flow velocity is reached. When flow is streamlined, concentric layers of fluid slip past each other with the slowest layers at the interface between blood and vessel wall. The fastest layers are in the center of the blood vessel. When the critical velocity is reached, turbulent flow results. In the presence of turbulent flow, flow does not increase as much for a given rise in pressure because energy is lost in the turbulence. The Reynolds number defines critical velocity.

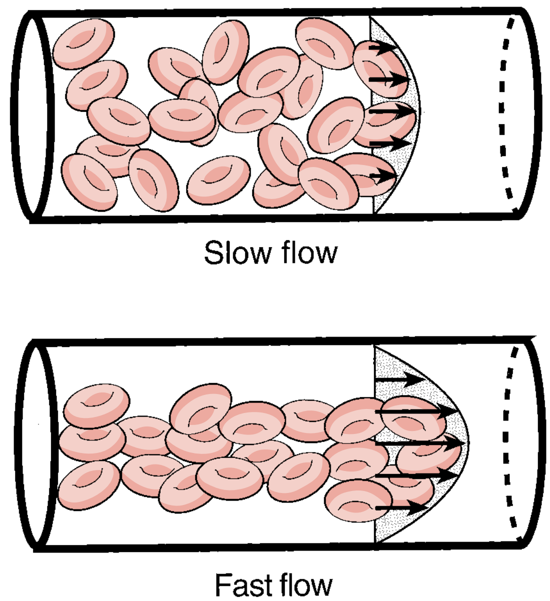


FIGURE 12.5 **Axial streaming and flow velocity.** The distribution of red blood cells in a blood vessel depends on flow velocity. As flow velocity increases, red blood cells move toward the center of the blood vessel (axial streaming), where velocity is highest. Axial streaming of red blood cells lowers the apparent viscosity of blood.

Finally, blood is not a strict **newtonian fluid,** a fluid that exhibits a constant viscosity regardless of flow velocity. When measured *in vitro*, the viscosity of blood decreases as the flow rate increases. This is because red cells tend to collect in the center of the lumen of a vessel as flow velocity increases, an arrangement known as **axial streaming** (Fig. 12.5). Axial streaming reduces the viscosity and, therefore, resistance to flow. Because this is a minor effect in the range of flow velocities in most blood vessels, we usually assume that the viscosity of blood (which is 3 to 4 times that of water) is independent of velocity.

PRESSURES IN THE CARDIOVASCULAR SYSTEM

Pressures in several regions of the cardiovascular system are readily measured and provide useful information. If arterial pressure is too high, it is a risk factor for cardiovascular diseases, including stroke and heart failure. When arterial pressure is too low, blood flow to vital organs is impaired.

Pressures in the various chambers of the heart are useful in evaluating cardiac function.

The Contractions of the Heart Produce Hemodynamic Pressure in the Aorta

The left ventricle imparts energy to the blood it ejects into the aorta, and this energy is responsible for the blood's circuit from the aorta back to the right side of the heart. Most of this energy is in the form of potential energy, which is the pressure referred to in Poiseuille's law. This is **hemodynamic pressure,** produced by contractions of the heart and stored in the elastic walls of the blood vessels. A much smaller component of the energy imparted by cardiac contractions is kinetic energy, which is the inertial energy associated with the movement of blood. The next section describes a third form of energy, hydrostatic pressure, derived from the force of gravity on blood.

A Column of Fluid Exerts Hydrostatic Pressure

Fluid standing in a container exerts pressure proportional to the height of the fluid above it. The pressure at a given depth depends only on the height of the fluid and its density and not on the shape of the container. This **hydrostatic pressure** is caused by the force of gravity acting on the fluid. When a person stands, blood pressure is greater in the vessels of the legs than in analogous vessels in the arms because hydrostatic pressure is added to hemodynamic pressure. The hydrostatic pressure difference is proportional to the height of the column of blood between the arms and legs.

Two conventions are observed when measuring blood pressure. First, ambient atmospheric pressure is used as a zero reference, so the mean arterial pressure is actually about 93 mm Hg above atmospheric pressure. Second, all cardiovascular pressures are referred to the level of the heart. This takes into account the fact that pressures vary depending on position because of the addition of hydrostatic to hemodynamic pressure. (As we will see in Chapter 16, when capillary pressure is discussed, the term *hydrostatic pressure* is used to mean hemodynamic plus hydrostatic pressure. Although this is not strictly correct, it is the conventional usage.)

Transmural Pressure Stretches Blood Vessels in Proportion to Their Compliance

Thus far, we have discussed pressure and flow in the cardiovascular system as if blood vessels were rigid tubes. But blood vessels are elastic, and they expand when the blood in them is under pressure. The degree to which a distensible vessel or container expands when it is filled with fluid is determined by the transmural pressure and its compliance. **Transmural pressure** (P_{TM}) is the difference between the pressure inside and outside a blood vessel:

$$P_{TM} = P_{inside} - P_{outside} \quad (5)$$

Compliance (C) is defined by the equation:

$$C = \Delta V/\Delta P_{TM} \quad (6)$$

where ΔV is the change in volume and ΔP_{TM} is the change in transmural pressure.

A more compliant structure exhibits a greater change in volume for a given transmural pressure change. The lower the compliance of a vessel, the greater the pressure that will result when a given volume is introduced. For example, each time the left ventricle contracts and ejects blood into the aorta, the aorta expands; in doing so, it exerts an elastic force on the increased volume of blood it contains. This force is measured as the pressure in the aorta. With aging, the aorta becomes less compliant, and aortic pressure rises more for a given increase in aortic volume. Veins, which have thinner walls, are much more compliant than arteries. This means that, when we stand up and increased hydrostatic pressure is exerted on both the veins and the arteries of the legs, the volume of the veins expands much more than that of the arteries.

Mean Arterial Pressure Depends on Cardiac Output and Systemic Vascular Resistance

A simple model is useful in seeing how the pressures, flows and volumes are established in the cardiovascular system. Imagine a circuit such as is shown in Figure 12.6. A pump propels fluid into stiff tubing that is of a large enough diameter to offer little resistance to flow. Midway around the circuit is a narrowing or stenosis of the tubing where almost all of the resistance to blood flow is located. The tubing downstream from the stenosis is 20 times more compliant than the tubing upstream from the stenosis. It has the same diameter as the upstream tubing and also offers almost no resistance to flow.

First imagine that the pump is turned off and the tubing is completely collapsed. At this point, enough fluid is infused into the circuit to fill all of the tubing and just begin to stretch the walls of the upstream and downstream tubing. Once the infused fluid comes to rest inside the tubing, the pressure inside the tubing is the same throughout because the pump is not adding energy to the circuit and there is no flow. The pressure inside the tubing is the pressure needed to "inflate" or fill the tubing in the resting state. The pressure outside the tubing is assumed to be atmospheric, and so the inside pressure equals the transmural pressure. Because the transmural pressure is the same throughout, and the left side of the circuit is made up of more compliant tubing, its volume is larger than the volume of the right side (see equation 6).

Imagine that the pump turns one cycle and shifts a small volume of fluid from the high-compliance tubing to the low-compliance tubing. The drop in volume on the left side has little effect on pressure because of its high compliance. However, an equivalent increase in volume on the low-compliance right side causes a 20-fold larger change in pressure. The pressure difference between the right and left side initiates flow from right to left. With only one stroke of the pump, the pressures on the two sides of the stenosis soon equalize as the volumes return to their resting values. At this point, flow ceases.

If the pump is turned on and left on, net volume is transferred from left to right until the pump has created

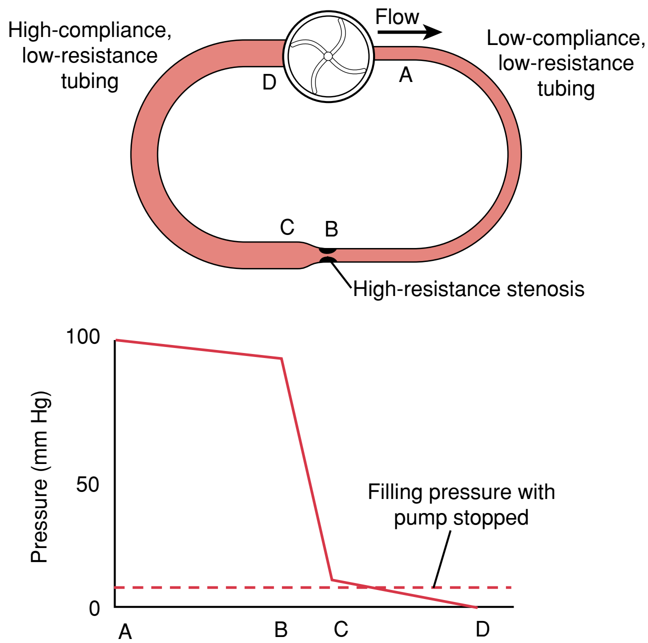


FIGURE 12.6 **A model of the systemic circulation.** When the pump is turned off, there is no flow and the pressures are the same everywhere in the circulation. This pressure is called the filling pressure, shown as a dotted line. When the pump is turned on, a small volume of fluid is transferred from the high compliance left-hand side (D) to the low compliance "arterial" side (A). This causes a small decrease in pressure in the left-hand tubing and a large increase in pressure in the right-hand tubing. The difference in the changes in pressures is because of the differences in compliance. Flow around the circulation occurs because of pressure difference established by transfer of fluid from the left- to the right-hand side of the model. Almost all of the resistance to flow is located at the high resistance stenosis between B and C. Because of this, almost all of the pressure drop occurs across the stenosis between B and C. This is shown by the pressures (solid line) observed when the pump is operating and the circulation is in a steady state.

a pressure difference sufficient to drive flow around the circuit equal to the output of the pump. In this new steady state, the pressure on the left side is slightly below the filling pressure and the pressure on the right side is much higher than the filling pressure. Although the volume removed from the right side exactly equals the volume added to the right side, the difference in the changes in pressures reflects the different compliances on the two sides of the pump.

The graph in Figure 12.6 shows that there is a small pressure drop from the outlet of the pump (A) to just before the stenosis (B), a large pressure drop occurs across the stenosis, and a very small pressure drop exists from just after the stenosis (C) to the inlet to the pump (D). This is because almost all of the resistance to flow is located at the stenosis between B and C.

In the steady state, flow (Q) through the circuit equals the rate at which volume is transferred from D to A by the pump. In the steady state, Q is also equal to the pressure difference between point A (P_A) and point D (P_D) divided by the resistance (R) to flow (see equation 1):

$$\text{Rate of pump transfer of volume from D to A} = Q = (P_A - P_D)/R \qquad (7)$$

We can think about the coupling of the output of the left heart to the flow through the systemic circulation in an analogous fashion. The systemic circulation is filled by a volume of blood that inflates the blood vessels. The pressure required to fill the blood vessels is the **mean circulatory filling pressure.** This pressure can be observed experimentally by temporarily stopping the heart long enough to let blood flow out of the arteries into the veins, until pressure is the same everywhere in the systemic circulation and flow ceases. When this is done, the pressure measured throughout the systemic circulation is approximately 7 mm Hg.

Just as in the model, when the heart restarts after temporarily stopping, a net volume of blood is transferred to the arterial side from the venous side of the systemic circulation. Net transfer continues until the pressure difference builds up in the aorta and decreases in the right atrium enough to create a pressure difference to drive the blood to the venous side of the circulation at a flow rate equal to the output from the left ventricle. Because the venous side of the systemic circulation is approximately 20 times more compliant than the arterial side, the increase in pressure on the arterial side is 20 times the drop in pressure on the venous side.

The pumping action of the heart in combination with the elasticity of the aorta and large arteries make the aortic and arterial pressures pulsatile. In this discussion, we will concern ourselves with the **mean arterial pressure** (P_a), the pulsatile pressure averaged over the cardiac cycle. Pressure in the aorta and large arteries is almost the same: there is only a 1 or 2 mm Hg pressure drop from the aorta to the large arteries. With vascular disease, the pressure drop in the large arteries can be much greater (see Clinical Focus Box 12.1). For most purposes, mean arterial pressure refers to the pressure measured in the aorta or any of the large arteries.

Flow through the aorta and large arteries (Q_{art}), and on to the rest of the systemic circulation, is equal to the cardiac output in the steady state. It is proportional to the difference between mean arterial pressure and pressure in the right atrium (right atrial pressure, P_{ra}). It is inversely proportional to the resistance to flow offered by the systemic circulation, the **systemic vascular resistance** (SVR). As stated earlier, most of this resistance to flow is located in the small arteries, arterioles, and capillaries. Physiological changes in SVR are primarily caused by changes in radius of small arteries and arterioles, the resistance vessels of the systemic circulation. This is discussed in more detail in Chapter 15. The relationship between cardiac output, flow through the aorta and large arteries, mean arterial pressure, and systemic vascular resistance is analogous to the model (equation 7):

$$\text{Cardiac output} = Q_{art} = (P_a - P_{ra})/\text{SVR} \qquad (8)$$

Systemic vascular resistance is calculated from cardiac output, mean arterial pressure, and right atrial pressure. Because right atrial pressure is normally close to zero and

CLINICAL FOCUS BOX 12.1

Effect of Vascular Disease on Arterial Resistance

The pressure gradient along large and medium-sized arteries, such as the aorta and renal arteries, is usually very small, due to the minimal resistance typically provided by these vessels. However, several disease processes can produce arterial narrowing and, thus, increase vascular resistance. Arterial narrowing exerts a profound effect on arterial blood flow because resistance varies inversely with the fourth power of the luminal radius.

The most common such disease is **atherosclerosis,** in which plaques composed of fatty substances (including cholesterol), fibrous tissue, and calcium form in the intimal layer of the artery. Atherosclerosis is the largest cause of morbidity and mortality in the United States: Myocardial infarction secondary to coronary atherosclerosis occurs more than 1 million times annually and accounts for over 700,000 deaths. Cerebrovascular infarction caused by carotid atherosclerosis is also a major cause of morbidity and mortality. Figure 12.A is an **arteriogram** from a patient with severe aortoiliac disease. The irregular luminal contour and focal narrowings of the iliac arteries (large arrowheads) and narrowing of the superior mesenteric artery (small arrowheads) are all caused by atherosclerosis.

FIGURE 12.A **An arteriogram of the abdominal aorta and iliac arteries, demonstrating atherosclerotic changes.**

Other disease processes, such as inflammation, blunt trauma, and clotting abnormalities can also lead to significant arterial narrowing or occlusion. One such entity, **fibromuscular dysplasia,** is a condition in which the blood vessel wall develops structural irregularities. Fibromuscular dysplasia can affect people of any age or gender, but most commonly involves young women. The arteriogram in Figure 12.B shows a series of narrowings in the renal artery caused by this dysplastic disease.

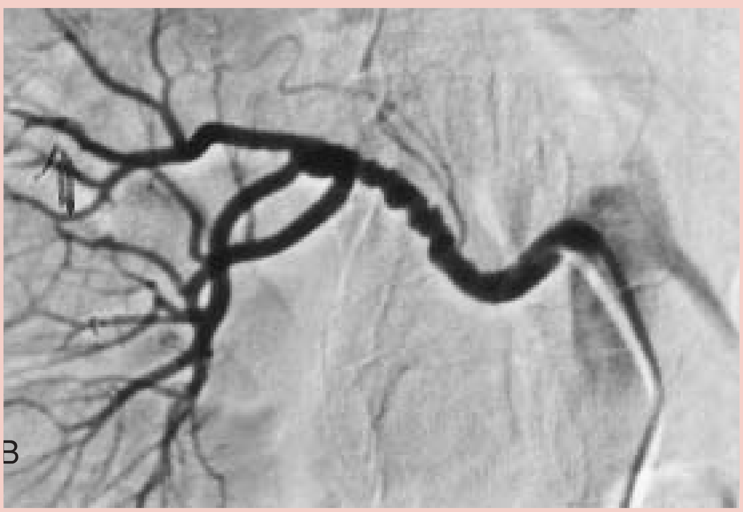


FIGURE 12.B **An arteriogram of the left renal artery, demonstrating changes of fibromuscular dysplasia.**

mean arterial pressure is much higher (e.g., 90 mm Hg), right atrial pressure is often ignored:

$$\text{Cardiac output} = Q_{art} = P_a/SVR \qquad (9)$$

Cardiac output and systemic vascular resistance are regulated physiologically. Their regulation allows control of mean arterial pressure. Regulation of cardiac output and systemic vascular resistance is discussed in subsequent chapters.

An assumption in the above discussion is that the right heart and pulmonary circulation faithfully transfer blood flow from the systemic veins to the left heart. In fact, coupling of the output of the right heart and the pulmonary circulation can be analyzed in the same terms as our discussion of the systemic circulation (the pulmonary circulation is discussed in Chapter 20). Our assumption that in the steady state, the outputs of the right and left hearts are exactly equal is true. However, transient differences between the outputs of the left and right heart occur and are physiologically important (see Chapter 14).

SYSTOLIC AND DIASTOLIC PRESSURES

Thus far, we have discussed only mean arterial pressure, despite the fact that the pumping of blood by the heart is a cyclic event. In a resting individual, the heart ejects blood into the aorta about once every second (i.e., the heart rate is about 60 beats/min). The phase during which cardiac muscle contracts is called **systole**, from the Greek for "a drawing together." During atrial systole, the pressures in the atria increase and push blood into the ventricles. During ventricular systole, pressures in the ventricles rise and the blood is pushed into the pulmonary artery or aorta. During **diastole** ("a drawing apart"), the cardiac muscle relaxes and the chambers fill from the venous side. Because of the pulsatile nature of the cardiac pump, pressure in the arterial system rises and falls with each heartbeat. The large arteries are distended when the pressure within them is increased (during systole), and they recoil when the ejection of blood falls during the latter phase of systole and ceases entirely during diastole. This recoil of the arteries sustains the flow of blood into the distal vasculature when there is no ventricular input of blood into the arterial system. The peak in systemic arterial pressure occurs during ventricular systole and is called **systolic pressure**. The nadir of systemic arterial pressure is called **diastolic pressure**. The difference between systolic pressure and diastolic pressure is the **pulse pressure.** We will discuss these three pressure types thoroughly in Chapter 15.

TRANSPORT IN THE CARDIOVASCULAR SYSTEM

The cardiovascular system depends on the energy provided by hemodynamic pressure gradients to move materials over long distances (bulk flow) and the energy provided by concentration gradients to move material over short distances (diffusion). Both types of movement are the result of differences in potential energy. As we have seen, bulk flow occurs because of differences in pressure. Diffusion occurs because of differences in chemical concentration.

Hemodynamic Pressure Gradients Drive Bulk Flow; Concentration Gradients Drive Diffusion

Blood circulation is an example of transport by **bulk flow**. This is an efficient means of transport over long distances, such as those between the legs and the lungs. **Diffusion** is accomplished by the random movement of individual molecules and is an effective transport mechanism over short distances. Diffusion occurs at the level of the capillaries, where the distances between blood and the surrounding tissue are short. The net transport of molecules by diffusion can occur within hundredths of a second or less when the distances involved are no more than a few microns. In contrast, minutes or hours would be needed for diffusion to occur over millimeters or centimeters.

Bulk Flow and Diffusion Are Influenced by Blood Vessel Size and Number

The aorta has the largest diameter of any artery, and the subsequent branches become progressively smaller down to the capillaries. Although the capillaries are the smallest blood vessels, there are several billion of them. For this reason, the total cross-sectional area of the lumens of all systemic capillaries (approximately 2,000 cm^2) greatly exceeds that of the lumen of the aorta (7 cm^2). In a steady state, the blood flow is equal at any two cross sections in series along the circulation. For example, the flow through the aorta is the same as the total flow through all of the systemic capillaries. Because the combined cross-sectional area of the capillaries is much greater and the total flow is the same, the velocity of flow in the capillaries is much lower. The slower movement of blood through the capillaries provides maximum opportunity for diffusional exchanges of substances between the blood and the tissue cells. In contrast, blood moves quickly in the aorta, where bulk flow, not diffusion, is important.

THE LYMPHATIC CIRCULATION

In vessels that are thin-walled and relatively permeable (e.g., capillaries and small venules), there is a net transfer of fluid out of the vessels and into the interstitial space. This fluid eventually returns from the interstitial space to the systemic circulation via another set of vessels, the **lymphatic vessels.** This movement of fluid from the systemic and pulmonary circulation into the interstitial space and then back to the systemic circulation via the lymphatic vessels is referred to as the **lymphatic circulation** (see Chapter 16). If the lymphatic circulation is interrupted, fluid accumulates in the interstitial space.

CONTROL OF THE CIRCULATION

The healthy cardiovascular system is capable of providing appropriate blood flow to each of the organs and tissues of the body under a wide range of conditions. This is done by

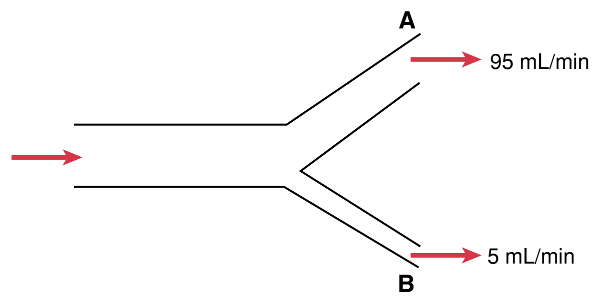
- Maintaining arterial blood pressure within normal limits
- Adjusting the output of the heart to the appropriate level
- Adjusting the resistance to blood flow in specific organs and tissues to meet special functional needs

The regulation of arterial pressure, cardiac output, and regional blood flow and capillary exchange is achieved by using a variety of neural, hormonal, and local mechanisms. In complex situations (e.g., standing or exercise), multiple mechanisms interact to regulate the cardiovascular response. In abnormal situations (e.g., heart failure), regulatory mechanisms that have evolved to handle normal events may be inadequate to restore proper function. The next few chapters describe these regulatory mechanisms in detail.

REVIEW QUESTIONS

DIRECTIONS: Each of the numbered items or incomplete statements in this section is followed by answers or by completions of the statement. Select the ONE lettered answer or completion that is BEST in each case.

1. Flow through a tube is proportional to the
   (A) Square of the radius
   (B) Square root of the length
   (C) Fourth power of the radius
   (D) Square of the length
   (E) Square root of the radius
2. Changes in transmural pressure
   (A) Can only be caused by changes in pressure inside a blood vessel
   (B) Cause changes in blood vessel volume, depending on the viscosity of the blood
   (C) Cause changes in blood vessel volume, depending on the compliance of the blood vessel
   (D) Cause proportional changes in blood flow
   (E) Are proportional to the length of a blood vessel
3. The pressure measured in either the arterial or the venous circulation when the heart has stopped long enough to allow the pressures to equalize is called the
   (A) Hemodynamic pressure
   (B) Mean arterial pressure
   (C) Transmural pressure
   (D) Mean circulatory filling pressure
   (E) Hydrostatic pressure
4. Blood flow becomes turbulent when
   (A) Flow velocity exceeds a certain value
   (B) Blood viscosity exceeds a certain value
   (C) Blood vessel diameter exceeds a certain value
   (D) Reynolds number exceeds a certain value
5. The volume of an aorta is increased by 30 mL with an associated pressure increase from 80 to 120 mm Hg. The compliance of the aorta is
   (A) 1.33 mm Hg/mL
   (B) 4.0 mm Hg/mL
   (C) 0.75 mm Hg/mL
   (D) 1.33 mL/mm Hg
   (E) 0.75 mL/mm Hg
6. In the tube in the diagram to the right, the inlet pressure is 75 mm Hg and the outlet pressure at A and B is 25 mm Hg. The resistance to flow is
   (A) 2 PRU
   (B) 0.5 PRU
   (C) 2 (mL/min)/mm Hg
   (D) 0.75 mm Hg/(mL/min)
   (E) 0.5 (mL/min)/mm Hg



SUGGESTED READING

Fung, YC. Biomechanics: Circulation. 2nd Ed. New York: Springer, 1997.Janicki JS, Sheriff DD, Robotham JL, Wise, RA. Cardiac output during exercise: Contributions of the cardiac, circulatory and respiratory systems. In: Rowell LB, Shepherd, JT, eds. Handbook of Physiology. Exercise: Regulation and Integration of Multiple Systems. New York: Oxford University Press, 1996;649–704.

Li JK-J. The Arterial Circulation. Totowa, NJ: Humana Press, 2000.

Rowell LB. Human Cardiovascular Control. New York: Oxford University Press, 1993.