

Objectives

- 1. Explain the principle physiological function of the pulmonary system.
- 2. Outline the major anatomical components of the respiratory system.
- 3. List major muscles involved in inspiration and expiration at rest and during exercise.
- 4. Discuss the importance of matching blood flow to alveolar ventilation in the lung.
- 5. Explain how gases are transported across the blood-gas interface in the lung.

Objectives

- 6. Discuss the major transportation modes of O_2 and CO_2 in the blood.
- 7. Discuss the effects of increasing temperature, decreasing pH, and increasing levels of 2–3 DPG on the oxygen-hemoglobin dissociation curve.
- 8. Describe the ventilatory response to constantload, steady-state exercise. What happens to ventilation if exercise is prolonged and performed in a high-temperature/humid environment?

Objectives

- Describe the ventilatory response to incremental exercise. What factors are thought to contribute to the alinear rise in ventilation at work rate above 50% to 70% of VO₂ max?
- 10. Identify the location and function of chemoreceptors and mechanoreceptors that are thought to play a role in the regulation of breathing.
- 11. Discuss the neural-humoral theory of respiratory control during exercise.

Introduction

- Pulmonary respiration
 - Ventilation
 - Exchange of O_2 and CO_2 in the lungs
- Cellular respiration
 - O₂ utilization and CO₂ production by the tissues
- Purposes of the respiratory system during exercise
 - Gas exchange between the environment and the body
 - Regulation of acid-base balance during exercise

pH Changes During Exercise

Blood pH

- Declines with increasing intensity exercise
 Muscle pH
- Declines more dramatically than blood pH
- Muscle has lower buffering capacity

Regulation of Acid-Base Balance

Lungs

- Increased blood PCO2
- Results in low pH
- Increases ventilation
- CO2 is "blown off"
- pH increases
- □ Kidneys
- – Regulate blood bicarbonate concentration
- – Important in long-term acid-base balance



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Larynx --Air passes over the larynx and down the trachea

Lung --Organ specialized for the exchange of gases between the blood and the atmosphere

Bronchus -- One of

the two primary divisions of the trachea that leads into the lungs Trachea --Windpipe; cartilage-reinforced tube extending from larynx to bronchi

Bronchiole -- A

thin-walled branch of a bronchus

Alveoli

--Clusters of air sacs that are the site of gas exchange for the human body

Function of the Lung

- Means of gas exchange between the external environment and the body
 - Replacing O₂
 - Removing CO₂
 - Regulation of acid-base balance
- Ventilation
 - Mechanical process of moving air into and out of lungs
- Diffusion
 - Random movement of molecules from an area of high concentration to an area of lower concentration

In Summary

 The primary function of the pulmonary system is to provide a means of gas exchange between the environment and the body. Further, the respiratory system plays an important role in the regulation of the acid-base balance during exercise.

Structure of the Respiratory System

• Organs

- Nose and nasal cavities
- Pharynx and larynx
- Trachea and bronchial tree
- Lungs
 - Alveoli
 - Site of gas exchange
- Diaphragm
 - Major muscle of inspiration

Structure of the Respiratory System

• Lungs are enclosed by membranes called pleura

- Visceral pleura
 - On outer surface of lung
- Parietal pleura
 - Lines the thoracic wall
- Intrapleural space
 - Intrapleural pressure is lower than atmospheric
 - Prevents collapse of alveoli

Major Organs of the Respiratory System





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Position of the Lungs, Diaphragm, and Pleura



Figure 10.2

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Conducting and Respiratory Zones

Conducting zone

- Conducts air to respiratory zone
- Humidifies, warms, and filters air
- Components:
 - Trachea
 - Bronchial tree
 - Bronchioles

Respiratory zone

- Exchange of gases between air and blood
- Components:
 - Respiratory bronchioles
 - Alveolar sacs
 - Surfactant prevents alveolar collapse

Structure of the Respiratory System

Conducting and Respiratory Zones



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100/

The Bronchial Tree





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Normal Inhalation

In Summary

 Anatomically, the pulmonary system consists of a group of passages that filter air and transport it into the lungs where gas exchange occurs within tiny air sacs called *alveoli*.

Mechanics of Breathing

- Movement of air occurs via bulk flow
 - Movement of molecules due to pressure difference
- Inspiration
 - Diaphragm pushes downward, ribs lift outward
 - Volume of lungs increases
 - Intrapulmonary pressure lowered
- Expiration
 - Diaphragm relaxes, ribs pulled downward
 - Volume of lungs decreases
 - Intrapulmonary pressure raised

The Mechanics of Inspiration and Expiration



250%

The Muscles of Respiration

Muscles of inspiration

Muscles of expiration



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A Closer Look 10.1 Respiratory Muscles and Exercise

- Do respiratory muscles fatigue during exercise?
 - Historically believed that respiratory muscles do not fatigue during exercise
 - Current evidence suggests that respiratory muscles do fatigue during exercise
 - Prolonged (>120 minutes)
 - High-intensity (90–100% VO₂ max)
- Do respiratory muscle adapt to training?
 - Yes!
 - Increased oxidative capacity improves respiratory muscle endurance
 - Reduced work of breathing

Airway Resistance

• Airflow depends on:

- Pressure difference between two ends of airway
- Resistance of airways

Airflow =
$$\frac{P_1 - P_2}{\text{Resistance}}$$

- Airway resistance depends on diameter
 - Chronic obstructive lung disease
 - Asthma and exercise-induced asthma

Clinical Applications 10.1 Exercise-Induced Asthma

Asthma results in bronchospasm

- Narrowing of airways
 - Increased work of breathing
 - Shortness of breath (dyspnea)
- Many potential causes

Exercise-induced asthma

- During or immediately following exercise
- May impair exercise performance

Clinical Applications 10.2 Exercise and Chronic Obstructive Lung Disease

- Chronic obstructive lung disease (COPD)
 - Increased airway resistance
 - Due to constant airway narrowing
 - Decreased expiratory airflow
- Includes two lung diseases:
 - Chronic bronchitis
 - Excessive mucus blocks airways
 - Emphysema
 - Airway collapse and increased resistance
- Increased work of breathing
 - Leads to shortness of breath
 - May interfere with exercise and activities of daily living

In Summary

- The major muscle of inspiration is the diaphragm. Air enters the pulmonary system due to intrapulmonary pressure being reduced below atmospheric pressure (bulk flow). At rest, expiration is passive. However, during exercise, expiration becomes active, using muscles located in the abdominal wall (e.g., rectus abdominis and internal oblique).
- The primary factor that contributes to airflow resistance in the pulmonary system is the diameter of the airway.

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Pulmonary Ventilation

- The amount of air moved in or out of the lungs per minute (V)
 - Tidal volume (V_T)
 - Amount of air moved per breath
 - Breathing frequency (f)
 - Number of breaths per minute

 $V = V_T x f$

- Alveolar ventilation (V_A)
 - Volume of air that reaches the respiratory zone
- Dead-space ventilation (V_D)
 - Volume of air remaining in conducting airways

 $\mathbf{V} = \mathbf{V}_{\mathsf{A}} + \mathbf{V}_{\mathsf{D}}$

In Summary

- Pulmonary ventilation refers to the amount of gas moved into and out of the lungs.
- The amount of gas moved per minute is the product of tidal volume times breathing frequency.

Pulmonary Volumes and Capacities

• Vital capacity (VC)

- Maximum amount of gas that can be expired after a maximum inspiration
- Residual volume (RV)
 - Volume of gas remaining in lungs after maximum expiration
- Total lung capacity (TLC)
 - Amount of gas in the lungs after a maximum inspiration.

Definitions of Pulmonary Volumes and Capacities

TABLE 10.1 Respiratory Volumes and Capacities for a 70-Kg Young Adult Male

| Measurement | Typical Value | Definition |
|------------------------------------|---------------|---|
| Respiratory Volumes | | |
| Tidal volume (TV) | 500 mL | Amount of air inhaled or exhaled in one breath during quiet breathing |
| Inspiratory reserve volume (IRV) | 3,000 mL | Amount of air in excess of tidal volume that can be inhaled with maximum effort |
| Expiratory reserve volume (ERV) | 1,200 mL | Amount of air in excess of tidal volume that can be exhaled with maximum effort |
| Residual volume (RV) | 1,300 mL | Amount of air remaining in the lungs after maximum expiration; that is, the amount of air that can never be voluntarily exhaled |
| Respiratory Capacities | | |
| Vital capacity (VC) | 4,700 mL | Amount of air that can be forcefully exhaled following a maximum inspiration VC = (ERV + TV + IRV) |
| Inspiratory capacity (IC) | 3,500 mL | Maximum amount of air that can be inhaled following a normal expiration (IC = $TV + IRV$) |
| Functional residual capacity (FRC) | 2,500 mL | Amount of air remaining in the lungs following a normal expiration (FRC = RV + ERV) |
| Total lung capacity (TLC) | 6,000 mL | Maximum amount of air in the lungs at the end of a maximum inspiration (TLC = $RV + VC$) |

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Lung Volumes and Capacities




Spirometry

- Measurement of pulmonary volumes and rate of expired airflow
- Useful for diagnosing lung diseases
 - Chronic obstructive lung disease (COPD)
- Spirometric tests
 - Vital capacity (VC)
 - Maximal volume of air that can be expired after maximal inspiration
 - Forced expiratory volume (FEV_1)
 - Volume of air expired in 1 second during maximal expiration
 - FEV₁/VC ratio
 - ≥80% is normal

A Computerized Spirometer



Figure 10.8

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Forced Expiratory Airflow Used to Diagnose Airway Obstruction



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In Summary

- Pulmonary volumes can be measured using spirometry.
- Vital capacity is the maximum amount of gas that can be expired after a maximal inspiration.
- Residual volume is the amount of gas left in the lungs after a maximal expiration.

Partial Pressure of Gases

Dalton's law

 The total pressure of a gas mixture is equal to the sum of the pressure that each gas would exert independently

 $P_{air} = PO_2 + PCO_2 + PN_2$

Calculation of partial pressure

| Gas | % in air | Fraction | | Barometric P | | Partial P |
|-----------------------|----------|----------|---|--------------|---|------------|
| O ₂ | 20.93 | 0.2093 | X | 760 mmHg | = | 159 mmHg |
| CO ₂ | 0.03 | 0.0003 | X | 760 mmHg | = | 0.3 mmHg |
| N_2 | 79.04 | 0.7904 | X | 760 mmHg | = | 600.7 mmHg |
| Total | 100 | | | | | 760 mmHg |

Diffusion of Gases

• Fick's law of diffusion

 The rate of gas transfer (V gas) is proportional to the tissue area, the diffusion coefficient of the gas, and the difference in the partial pressure of the gas on the two sides of the tissue, and inversely proportional to the thickness.

V gas =
$$\frac{A}{T} \times D \times (P_1 - P_2)$$

- V gas = rate of diffusion
- A = tissue area
- T = tissue thickness
- D = diffusion coefficient of gas
- $P_1 P_2$ = difference in partial pressure

Chapter 10

Partial Pressures of O₂ and CO₂ and Gas Exchange



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In Summary

- Gas moves across the blood-gas interface in the lung due to simple diffusion.
- The rate of diffusion is described by Fick's law, which states: the volume of gas that moves across a tissue is proportional to the area for diffusion and the difference in partial pressure across the membrane, and is inversely proportional to membrane thickness.

Blood Flow to the Lung

Pulmonary circuit

- Same rate of flow as systemic circuit
- Lower pressure
- When standing, most of the blood flow is to the base of the lung
 - Due to gravitational force
- During exercise, more blood flow to apex

Chapter 10

The Pulmonary and Systemic Circulation





Regional Blood Flow within the Lung





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In Summary

- The pulmonary circulation is a low-pressure system with a rate of blood flow equal to that in the systemic circuit.
- In a standing position, most of the blood flow to the lung is distributed to the base of the lung due to gravitational force.

Ventilation-Perfusion Relationships

- Ventilation/perfusion ratio (V/Q)
 - Indicates matching of blood flow to ventilation
 - Ideal: ~1.0
- Apex of lung
 - Underperfused (ratio <1.0)
- Base of lung
 - Overperfused (ratio >1.0)
- During exercise
 - Light exercise improves V/Q ratio
 - Heavy exercise results in V/Q inequality

Ventilation/Perfusion Ratios



In Summary

- Efficient gas exchange between the blood and the lung requires proper matching of blood flow to ventilation (called ventilation-perfusion relationships).
- The ideal ratio of ventilation to perfusion is 1.0 or slightly greater, since this ratio implies a perfect matching on blood flow to ventilation.

O₂ Transport in the Blood

- 99% of O₂ is transported bound to hemoglobin (Hb)
 - Oxyhemoglobin: Hb bound to O₂
 - Deoxyhemoglobin: Hb not bound to O_2
- Amount of O₂ that can be transported per unit volume of blood is dependent on the Hb concentration
 - Each gram of Hb can transport 1.34 ml O_2
- Oxygen content of blood (100% Hb saturation)
 - Males:

150 g Hb/L blood x 1.34 ml O_2/g Hb = 200 ml O_2/L blood

– Females:

130 g Hb/L blood x 1.34 ml O_2/g Hb = 174 ml O_2/L blood

Oxyhemoglobin Dissociation Curve

- Deoxyhemoglobin + $O_2 \leftrightarrow Oxyhemoglobin$
- Direction of reaction depends on:
 - $-PO_2$ of the blood
 - Affinity between Hb and O₂
- At the lung
 - High PO_2 = formation of oxyhemoglobin
- At the tissues
 - Low PO_2 = release of O_2 to tissues

Oxygen-Hemoglobin Dissociation Curve



Effect of pH, Temperature, and 2–3 DPG on the O₂-Hb Dissociation Curve

• pH

- Decreased pH lowers Hb-O₂ affinity
- Results in a "rightward" shift of the curve
 - Favors "offloading" of O₂ to the tissues

Temperature

- Increased blood temperature lowers Hb-O₂ affinity
- Results in a "rightward" shift of the curve

• 2–3 DPG

- Byproduct of RBC glycolysis
- May result in a "rightward" shift of the curve
 - During altitude exposure
 - Not a major cause of rightward shift during exercise

O₂ and CO₂ Transport in Blood

Figure 10.15

Effect of pH on the Oxygen-Hemoglobin Dissociation Curve





O₂ and CO₂ Transport in Blood

Chapter 10

Effect of Temperature on the Oxygen-Hemoglobin Dissociation Curve





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O₂ Transport in Muscle

- Myoglobin (Mb)
 - Shuttles O₂ from the cell membrane to the mitochondria
- Mb has a higher affinity for O₂ than hemoglobin
 - Even at low PO₂
 - Allows Mb to store O₂
 - O₂ reserve for muscle

Dissociation Curves for Myoglobin and Hemoglobin



Figure 10.18

CO₂ Transport in Blood

- Dissolved in plasma (10%)
- Bound to Hb (20%)
- Bicarbonate (70%)

 $CO_2 + H_2O$ Carbonic anhydrase

- $H_2CO_3 \longrightarrow H^+ + HCO_3^-$
- At the tissue:
 - H⁺ binds to Hb
 - HCO₃⁻ diffuses out of RBC into plasma
 - CI⁻ diffuses into RBC (chloride shift)
- At the lung:
 - O₂ binds to Hb (drives off H⁺)
 - Reaction reverses to release CO₂

Figure 10.19

CO₂ Transport in the Blood at the Tissue



CO₂ Transport in the Blood at the Lung



Figure 10.20

In Summary

- Over 99% of the O₂ transported in blood is chemically bonded with hemoglobin. The effect of the partial pressure of O₂ on the combination of O₂ with hemoglobin is illustrated by the S-shaped O₂-hemoglobin dissociation curve.
- An increase in body temperature and a reduction in blood pH results in a right shift in the O₂-hemoglobin dissociation curve and a reduced affinity of hemoglobin for O₂.

In Summary

Carbon dioxide is transported in blood three forms: (1) dissolved CO₂ (10% of CO₂ is transported in this way), (2) CO₂ bound to hemoglobin (called carbamino-hemoglobin; about 20% of blood CO₂ is transported via this form), and (3) bicarbonate (70% of CO₂ found in the blood is transported as bicarbonate [HCO₃⁻]).

Ventilation and Acid-Base Balance

 Pulmonary ventilation removes H⁺ from blood by the HCO₃⁻ reaction

 $\begin{array}{l} {\color{black} \leftarrow} & {\color{black} Lung} \\ CO_2 + H_2O \xleftarrow{} & {\color{black} Carbonic anhydrase} \\ {\color{black} H_2CO_3} \longleftrightarrow {\color{black} H^+ + HCO_3^-} \\ \\ {\color{black} Muscle} \end{array}$

- Increased ventilation results in CO₂ exhalation
 - Reduces PCO₂ and H⁺ concentration (pH increase)
- Decreased ventilation results in buildup of CO₂
 - Increases PCO₂ and H⁺ concentration (pH decrease)

In Summary

 An increase in pulmonary ventilation causes exhalation of additional CO₂, which results in a reduction of blood PCO₂ and a lowering of hydrogen ion concentration (i.e., pH increases).

Rest-to-Work Transitions

• At the onset of constant-load submaximal exercise:

- Initially, ventilation increases rapidly
 - Then, a slower rise toward steady state
- $-PO_2$ and PCO_2 are relatively unchanged
 - Slight decrease in PO₂ and increase in PCO₂

Figure 10.21

The Transition From Rest to Exercise



d.

Prolonged Exercise in a Hot Environment

- During prolonged submaximal exercise in a hot/humid environment:
 - Ventilation tends to drift upward
 - Increased blood temperature affects respiratory control center
 - Little change in PCO₂

Exercise in a Hot/Humid Environment



Incremental Exercise in an Untrained Subject

Ventilation

- Linear increase up to ~50–75% VO_2 max
- Exponential increase beyond this point
- Ventilatory threshold (Tvent)
 - Inflection point where V_E increases exponentially
- **PO**₂
 - Maintained within 10–12 mmHg of resting value

Incremental Exercise in an Elite Athlete

- Ventilation
 - Tvent occurs at higher % VO₂ max
- PO₂
 - Decrease of 30-40 mmHg at near-maximal work
 - Hypoxemia
 - Due to:
 - Ventilation/perfusion mismatch
 - Short RBC transit time in pulmonary capillary due to high cardiac output
Ventilatory and Blood-Gas Responses to Exercise

Ventilatory Response to Incremental Exercise



- At the onset of constant-load submaximal exercise, ventilation increases rapidly, followed by a slower rise toward a steady-state value. Arterial PO₂ and PCO₂ are maintained relatively constant during this type of exercise.
- During prolonged exercise in a hot/humid environment, ventilation "drifts" upward due to the influence of rising body temperature on the respiratory control center.
- Incremental exercise results in a linear increase in V_E up to approximately 50% to 70% of O₂ max; at higher work rates, ventilation begins to rise exponentially. This ventilatory inflection point has been called the ventilatory threshold.

Control of Ventilation at Rest

- Inspiration and expiration
 - Produced by contraction and relaxation of diaphragm
- Controlled by somatic motor neurons in the spinal cord
 - Controlled by respiratory control center
 - In medulla oblongata

Respiratory Control Center

- Stimulus for inspiration comes from four respiratory rhythm centers
 - In Medulla
 - preBötzinger Complex and retrotrapezoidal nucleus
 - In Pons
 - Pneumotaxic center and caudal pons

Input to the Respiratory Control Center

- Humoral chemoreceptors
 - Central chemoreceptors
 - Located in the medulla
 - PCO₂ and H⁺ concentration in cerebrospinal fluid
 - Peripheral chemoreceptors
 - Aortic and carotid bodies
 - PO₂, PCO₂, H⁺, and K⁺ in blood
- Neural input
 - From motor cortex and skeletal muscle mechanoreceptors

The Brain Stem Respiratory Control Centers



The Location of the Peripheral Chemoreceptors





Effect of Arterial PCO₂ on Ventilation





Effect of Arterial PO₂ on Ventilation





Ventilatory Control During Exercise

Submaximal exercise

- Primary drive:
 - Higher brain centers (central command)
- "Fine tuned" by:
 - Humoral chemoreceptors
 - Neural feedback from muscle

Heavy exercise

- Alinear rise in V_E
 - Increasing blood H⁺ (from lactic acid) stimulates carotid bodies
 - Also K⁺, body temperature, and blood catecholamines may contribute

Chapter 10

Figure 10.27

A Summary of Respiratory Control During Submaximal Exercise



*Act to fine-tune ventilation during exercise

A Closer Look 10.2 Training Reduces the Ventilatory Response to Exercise

- No effect on lung structure
- Ventilation is lower during exercise following training
 - Exercise ventilation is 20–30% lower at same submaximal work rate
- Mechanism:
 - Changes in aerobic capacity of locomotor muscles
 - Result in less production of lactic acid
 - Less afferent feedback from muscle to stimulate breathing

Figure 10.29

Effects of Endurance Training on Ventilation During Exercise

Training Reduces Exercise Ventilation



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Current evidence suggests that the normal rhythm of breathing is generated by the interaction between four separate respiratory rhythm centers located in the medulla oblongata and the pons. At rest, the breathing rhythm is dominated by pacemaker neurons in the preBötzinger Complex. During exercise, however, the preBötzinger Complex interacts with the retrotrapezoidal nucleus along with two additional regulatory centers in the Pons to regulate breathing. The coupling of these respiratory control centers to regulate breathing involves both positive and negative feedback to achieve tight control.

Input into the respiratory control center to increase ventilation can come from both neural and humoral sources. Neural input may come from higher brain centers, or it may arise from receptors in the exercising muscle. Humoral input may arise from central chemoreceptors, peripheral chemoreceptors, and/or lung CO₂ receptors. The central chemoreceptors are sensitive to increases in PCO₂ and decreases in pH. The peripheral chemoreceptors (carotid bodies are the most important) are sensitive to increases in PCO₂ and decreases in PO₂ or pH. Receptors in the lung that are sensitive to an increase in PCO₂ are hypothesized to exist.

- The primary drive to increase ventilation during exercise probably comes from higher brain centers (central command). Also, humoral chemoreceptors and neural feedback from working muscles act to fine-tune ventilation.
- Controversy exists concerning the mechanism to explain the alinear rise in ventilation (ventilatory threshold) that occurs during an incremental exercise test. However, it appears that the rise in blood H⁺ concentration that occurs during this type of exercise provides the principal stimulus to increase ventilation via stimulation of the carotid bodies.

Effect of Training on Ventilation

- No effect on lung structure and function at rest
- Normal lung exceeds demand for gas exchange
 - Adaptation is not required for the lung to maintain blood-gas homeostasis
- One exception: Elite endurance athletes
 - Failure of lung to adapt to training results in hypoxemia

Chapter 10

Does the Pulmonary System Limit Exercise Performance?

- Low-to-moderate intensity exercise
 - Pulmonary system not seen as a limitation

Maximal exercise

- Historically not thought to be a limitation in healthy individuals at sea level
 - New evidence that respiratory muscle fatigue does occur during high intensity exercise (>90% VO₂ max)
- May be limiting in elite endurance athletes
 - 40–50% experience hypoxemia

Research Focus 10.1 Do Nasal Strips Improve Athletic Performance?

- The purpose of nasal strips
 - Reduce nostril airway resistance
- Theoretically, would increase airflow into lungs
 - No evidence of increased ventilation or performance
- Potential psychological advantage

- The pulmonary system does not limit exercise performance in healthy young subjects during prolonged submaximal exercise (e.g., work rates <90% VO₂ max).
- In contrast to submaximal exercise, new evidence indicates that the respiratory system (i.e., respiratory muscle fatigue) may be a limiting factor in exercise performance at work rates >90% VO₂ max. Further, incomplete pulmonary gas exchange may occur in some elite athletes and limit exercise performance at high exercise intensities.

Study Questions

- 1. What is the primary function of the pulmonary system? What secondary function does it serve?
- 2. List and discuss the major anatomical components of the respiratory system.
- 3. What muscle groups are involved in ventilation during rest? During exercise?
- 4. What is the functional significance of the ventilationperfusion ratio? How would a high V/Q ratio affect gas exchange in the lung?
- 5. Discuss the factors that influence the rate of diffusion across the blood-gas interface in the lung.

Study Questions

- 6. Graph the relationship between hemoglobin- O_2 saturation and the partial pressure of O_2 in the blood. What is the functional significance of the shape of the O_2 -hemoglobin dissociation curve? What factors affect the shape of the curve?
- 7. Discuss the modes of transportation for CO_2 in the blood.
- 8. Graph the ventilatory response in the transition from rest to constant-load submaximal exercise. What happens to ventilation if the exercise is prolonged and performed in a hot/humid environment? Why?
- 9. Graph the ventilatory response to incremental exercise. Label the ventilatory threshold. What factor(s) might explain the ventilatory threshold?

Study Questions

- 10. List and identify the functions of the chemoreceptors that contribute to the control of breathing.
- 11. What neural afferents might also contribute to the regulation of ventilation during exercise?
- 12. Discuss the control of ventilation during exercise.