Movement	Target	Target motion direction	Prime mover	Origin	Insertion
Axial muscles					
Brings elbows together; moves elbow up (as during an uppercut punch)	Humerus	Flexion; adduction; medial rotation	Pectoralis major	Clavicle; sternum; cartilage of certain ribs (1–6 or 1–7); aponeurosis of external oblique muscle	Greater tubercle of humerus
Moves elbow back (as in elbowing someone standing behind you); spreads elbows apart	Humerus; scapula	Humerus: extension, adduction, and medial rotation; scapula: depression	Latissimus dorsi	Thoracic vertebrae (T7–T12); lumbar vertebrae; lower ribs (9–12); iliac crest	Intertubercular sulcus of humerus
Scapular muscles					
Lifts arms at shoulder	Humerus	Abduction; flexion; extension; medial and lateral rotation	Deltoid	Trapezius; clavicle; acromion; spine of scapula	Deltoid tuberosity of humerus
Assists pectoralis major in bringing elbows together and stabilizes shoulder joint during movement of the pectoral girdle	Humerus	Medial rotation	Subscapularis	Subscapular fossa of scapula	Lesser tubercle of humerus
Rotates elbow outwards, as during a tennis swing	Humerus	Abduction	Supraspinatus	Supraspinous fossa of scapula	Greater tubercle of humerus
Rotates elbow outwards, as during a tennis swing	Humerus	Extension; adduction	Infraspinatus	Infraspinous fossa of scapula	Greater tubercle of humerus
Assists with medial rotation at the shoulder	Humerus	Extension; adduction	Teres major	Posterior surface of scapula	Intertubercular sulcus of humerus
Assists infraspinatus in rotating elbow outwards	Humerus	Extension; adduction	Teres minor	Lateral border of dorsal scapular surface	Greater tubercle of humerus
Moves elbow up and across body, as when putting hand on chest	Humerus	Flexion; adduction	Coracobra chialis	Coracoid process of scapula	Medial surface of humerus shaft

FIGURE 11.24 **Muscles That Move the Humerus**

The rest of the shoulder muscles originate on the scapula. The anatomical and ligamental structure of the shoulder joint and the arrangements of the muscles covering it, allows the arm to carry out different types of movements. The **deltoid**, the thick muscle that creates the rounded lines of the shoulder is the major abductor of the arm, but it also facilitates flexing and medial rotation, as well as extension and lateral rotation. The **subscapularis** originates on the anterior scapula and medially rotates the arm. Named for their locations, the **supraspinatus** (superior to the spine of the scapula) and the **infraspinatus** (inferior to the spine of the scapula) abduct the arm, and laterally rotate the arm, respectively. The thick and flat **teres major** is inferior to the teres minor and extends the arm, and assists in adduction and medial rotation of it. The long **teres minor** laterally rotates and extends the arm. Finally, the **coracobrachialis** flexes and adducts the arm.

The tendons of the deep subscapularis, supraspinatus, infraspinatus, and teres minor connect the scapula to the humerus, forming the **rotator cuff** (musculotendinous cuff), the circle of tendons around the shoulder joint. When baseball pitchers undergo shoulder surgery it is usually on the rotator cuff, which becomes pinched and inflamed, and may tear away from the bone due to the repetitive motion of bring the arm overhead to throw a fast pitch.

Muscles That Move the Forearm

The forearm, made of the radius and ulna bones, has four main types of action at the hinge of the elbow joint:

flexion, extension, pronation, and supination. The forearm flexors include the biceps brachii, brachialis, and brachioradialis. The extensors are the **triceps brachii** and **anconeus**. The pronators are the **pronator teres** and the **pronator quadratus**, and the **supinator** is the only one that turns the forearm anteriorly. When the forearm faces anteriorly, it is supinated. When the forearm faces posteriorly, it is pronated.

The biceps brachii, brachialis, and brachioradialis flex the forearm. The two-headed **biceps brachii** crosses the shoulder and elbow joints to flex the forearm, also taking part in supinating the forearm at the radioulnar joints and flexing the arm at the shoulder joint. Deep to the biceps brachii, the **brachialis** provides additional power in flexing the forearm. Finally, the **brachioradialis** can flex the forearm quickly or help lift a load slowly. These muscles and their associated blood vessels and nerves form the **anterior compartment of the arm** (anterior flexor compartment of the arm) (Figure 11.25 and Figure 11.26).

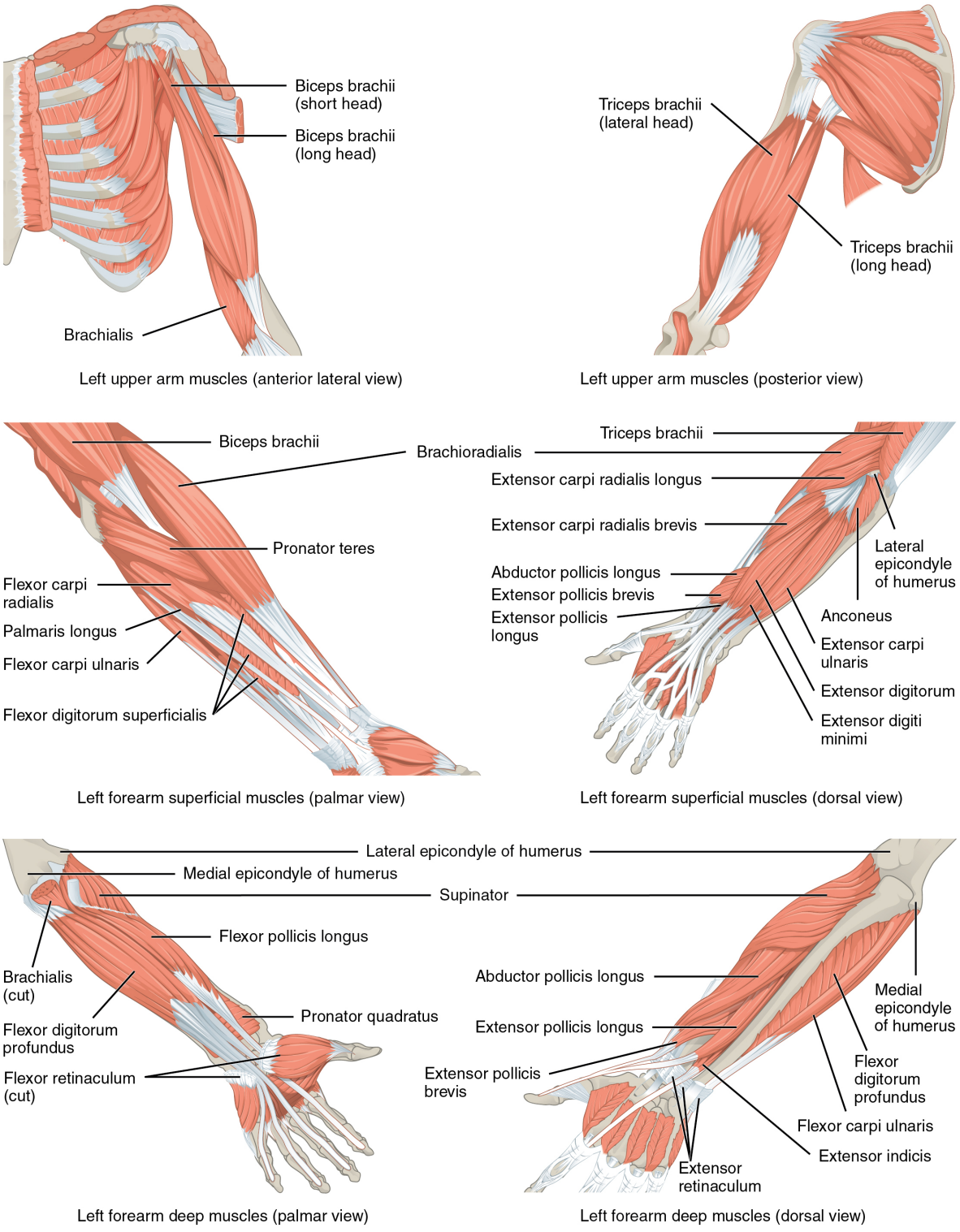


FIGURE 11.25 Muscles That Move the Forearm The muscles originating in the upper arm flex, extend, pronate, and supinate the forearm. The muscles originating in the forearm move the wrists, hands, and fingers.

Movement	Target	Target motion direction	Prime mover	Origin	Insertion
Anterior muscles (flexion)					
Performs a bicep curl; also allows palm of hand to point toward body while flexing	Forearm	Flexion; supination	Biceps brachii	Coracoid process; tubercle above glenoid cavity	Radial tuberosity
	Forearm	Flexion	Brachialis	Front of distal humerus	Coronoid process of ulna
Assists and stabilizes elbow during bicep-curl motion	Forearm	Flexion	Brachioradialis	Lateral supracondylar ridge at distal end of humerus	Base of styloid process of radius
Posterior muscles (extension)					
Extends forearm, as during a punch	Forearm	Extension	Triceps brachii	Infraglenoid tubercle of scapula; posterior shaft of humerus; posterior humeral shaft distal to radial groove	Olecranon process of ulna
Assists in extending forearm; also allows forearm to extend away from body	Forearm	Extension; abduction	Anconeus	Lateral epicondyle of humerus	Lateral aspect of olecranon process of ulna
Anterior muscles (pronation)					
Turns hand palm-down	Forearm	Pronation	Pronator teres	Medial epicondyle of humerus; coronoid process of ulna	Lateral radius
Assists in turning hand palm-down	Forearm	Pronation	Pronator quadratus	Distal portion of anterior ulnar shaft	Distal surface of anterior radius
Posterior muscles (supination)					
Turns hand palm-up	Forearm	Supination	Supinator	Lateral epicondyle of humerus; proximal ulna	Proximal end of radius

FIGURE 11.26 **Muscles That Move the Forearm**

Muscles That Move the Wrist, Hand, and Fingers

Wrist, hand, and finger movements are facilitated by two groups of muscles. The forearm is the origin of the **extrinsic muscles of the hand**. The palm is the origin of the intrinsic muscles of the hand.

Muscles of the Arm That Move the Wrists, Hands, and Fingers

The muscles in the **anterior compartment of the forearm** (anterior flexor compartment of the forearm) originate on the humerus and insert onto different parts of the hand. These make up the bulk of the forearm. From lateral to medial, the **superficial anterior compartment of the forearm** includes the **flexor carpi radialis**, **palmaris longus**, **flexor carpi ulnaris**, and **flexor digitorum superficialis**. The flexor digitorum superficialis flexes the hand as well as the digits at the knuckles, which allows for rapid finger movements, as in typing or playing a musical instrument (see Figure 11.27 and Table 11.9). However, poor ergonomics can irritate the tendons of these muscles as they slide back and forth with the carpal tunnel of the anterior wrist and pinch the median nerve, which also travels through the tunnel, causing Carpal Tunnel Syndrome. The **deep anterior compartment** produces flexion and bends fingers to make a fist. These are the **flexor pollicis longus** and the **flexor digitorum profundus**.

The muscles in the **superficial posterior compartment of the forearm** (superficial posterior extensor compartment of the forearm) originate on the humerus. These are the **extensor radialis longus**, **extensor carpi radialis brevis**, **extensor digitorum**, **extensor digiti minimi**, and the **extensor carpi ulnaris**.

The muscles of the **deep posterior compartment of the forearm** (deep posterior extensor compartment of the forearm) originate on the radius and ulna. These include the **abductor pollicis longus**, **extensor pollicis brevis**,

extensor pollicis longus, and **extensor indicis** (see Figure 11.27).

Movement	Target	Target motion direction	Prime mover	Origin	Insertion
Superficial anterior compartment of forearm					
Bends wrist toward body; tilts hand to side away from body	Wrist; hand	Flexion; abduction	Flexor carpi radialis	Medial epicondyle of humerus	Base of second and third metacarpals
Assists in bending hand up toward shoulder	Wrist	Flexion	Palmaris longus	Medial epicondyle of humerus	Palmar aponeurosis; skin and fascia of palm
Assists in bending hand up toward shoulder; tilts hand to side away from body; stabilizes wrist	Wrist; hand	Flexion, adduction	Flexor carpi ulnaris	Medial epicondyle of humerus; olecranon process; posterior surface of ulna	Pisiform, hamate bones, and base of fifth metacarpal
Bends fingers to make a fist	Wrist; fingers 2–5	Flexion	Flexor digitorum superficialis	Medial epicondyle of humerus; coronoid process of ulna; shaft of radius	Middle phalanges of fingers 2–5
Deep anterior compartment of forearm					
Bends tip of thumb	Thumb	Flexion	Flexor pollicis longus	Anterior surface of radius; interosseous membrane	Distal phalanx of thumb
Bends fingers to make a fist; also bends wrist toward body	Wrist; fingers	Flexion	Flexor digitorum profundus	Coronoid process; anteromedial surface of ulna; interosseous membrane	Distal phalanges of fingers 2–5
Superficial posterior compartment of forearm					
Straightens wrist away from body; tilts hand to side away from body	Wrist	Extension; abduction	Extensor radialis longus	Lateral supracondylar ridge of humerus	Base of second metacarpal
Assists extensor radialis longus in extending and abducting wrist; also stabilizes hand during finger flexion.	Wrist	Extension, abduction	Extensor carpi radialis brevis	Lateral epicondyle of humerus	Base of third metacarpal
Opens fingers and moves them sideways away from the body	Wrist; fingers	Extension; abduction	Extensor digitorum	Lateral epicondyle of humerus	Extensor expansions; distal phalanges of fingers
Extends little finger	Little finger	Extension	Extensor digiti minimi	Lateral epicondyle of humerus	Extensor expansion; distal phalanx of finger 5
Straightens wrist away from body; tilts hand to side toward body	Wrist	Extension; adduction	Extensor carpi ulnaris	Lateral epicondyle of humerus; posterior border of ulna	Base of fifth metacarpal
Deep posterior compartment of forearm					
Moves thumb sideways toward body; extends thumb; moves hand sideways toward body	Wrist; thumb	Thumb: abduction, extension; wrist: abduction	Abductor pollicis longus	Posterior surface of radius and ulna; interosseous membrane	Base of first metacarpal; trapezium
Extends thumb	Thumb	Extension	Extensor pollicis brevis	Dorsal shaft of radius and ulna; interosseous membrane	Base of proximal phalanx of thumb
Extends thumb	Thumb	Extension	Extensor pollicis longus	Dorsal shaft of radius and ulna; interosseous membrane	Base of distal phalanx of thumb
Extends index finger; straightens wrist away from body	Wrist; index finger	Extension	Extensor indicis	Posterior surface of distal ulna; interosseous membrane	Tendon of extensor digitorum of index finger

FIGURE 11.27 Muscles That Move the Wrist, Hands, and Forearm

The tendons of the forearm muscles attach to the wrist and extend into the hand. Fibrous bands called **retinacula** sheath the tendons at the wrist. The **flexor retinaculum** extends over the palmar surface of the hand while the **extensor retinaculum** extends over the dorsal surface of the hand.

Intrinsic Muscles of the Hand

The **intrinsic muscles of the hand** both originate and insert within it (Figure 11.28). These muscles allow your fingers to also make precise movements for actions, such as typing or writing. These muscles are divided into three

groups. The **thenar** muscles are on the radial aspect of the palm. The **hypothenar** muscles are on the medial aspect of the palm, and the **intermediate** muscles are midpalmar.

The thenar muscles include the **abductor pollicis brevis**, **opponens pollicis**, **flexor pollicis brevis**, and the **adductor pollicis**. These muscles form the **thenar eminence**, the rounded contour of the base of the thumb, and all act on the thumb. The movements of the thumb play an integral role in most precise movements of the hand.

The hypothenar muscles include the **abductor digiti minimi**, **flexor digiti minimi brevis**, and the **opponens digiti minimi**. These muscles form the **hypothenar eminence**, the rounded contour of the little finger, and as such, they all act on the little finger. Finally, the intermediate muscles act on all the fingers and include the **lumbrical**, the **palmar interossei**, and the **dorsal interossei**.

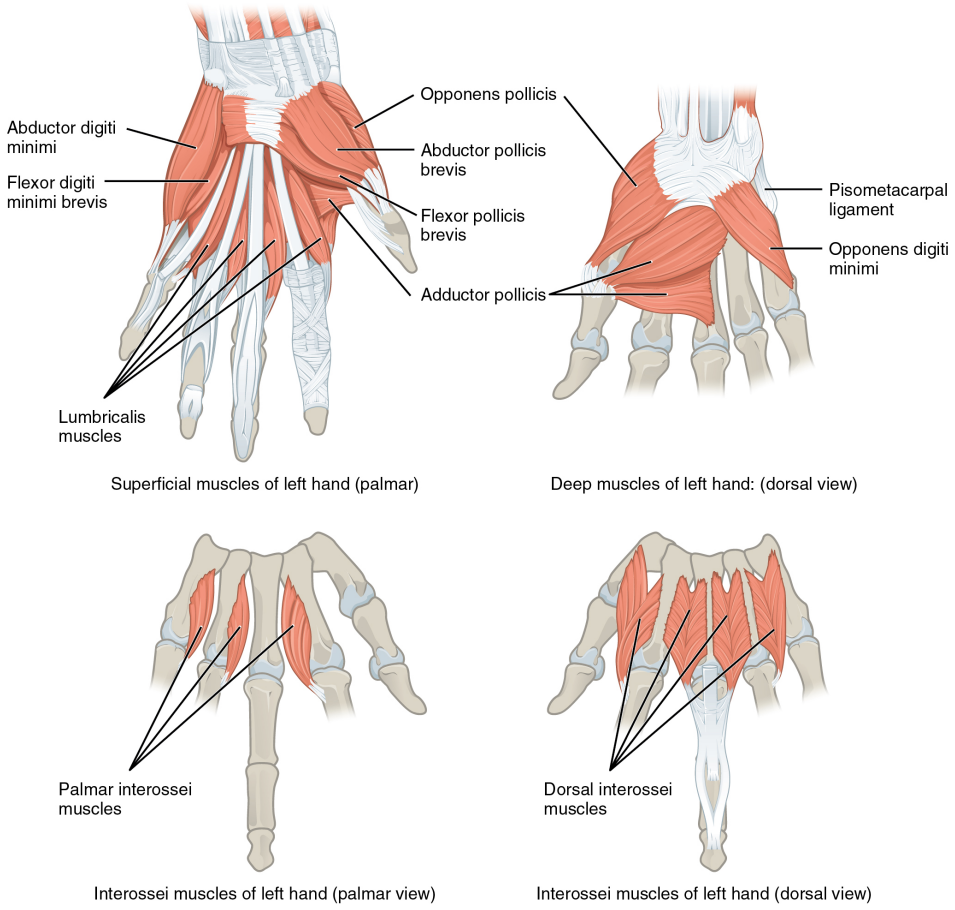


FIGURE 11.28 Intrinsic Muscles of the Hand The intrinsic muscles of the hand both originate and insert within the hand. These muscles provide the fine motor control of the fingers by flexing, extending, abducting, and adducting the more distal finger and thumb segments.

Intrinsic Muscles of the Hand

Muscle	Movement	Target	Target motion direction	Prime mover	Origin	Insertion
Thenar muscles	Moves thumb toward body	Thumb	Abduction	Abductor pollicis brevis	Flexor retinaculum; and nearby carpals	Lateral base of proximal phalanx of thumb
Thenar muscles	Moves thumb across palm to touch other fingers	Thumb	Opposition	Opponens pollicis	Flexor retinaculum; trapezium	Anterior of first metacarpal
Thenar muscles	Flexes thumb	Thumb	Flexion	Flexor pollicis brevis	Flexor retinaculum; trapezium	Lateral base of proximal phalanx of thumb
Thenar muscles	Moves thumb away from body	Thumb	Adduction	Adductor pollicis	Capitate bone; bases of metacarpals 2–4; front of metacarpal 3	Medial base of proximal phalanx of thumb
Hypothenar muscles	Moves little finger toward body	Little finger	Abduction	Abductor digiti minimi	Pisiform bone	Medial side of proximal phalanx of little finger
Hypothenar muscles	Flexes little finger	Little finger	Flexion	Flexor digiti minimi brevis	Hamate bone; flexor retinaculum	Medial side of proximal phalanx of little finger
Hypothenar muscles	Moves little finger across palm to touch thumb	Little finger	Opposition	Opponens digiti minimi	Hamate bone; flexor retinaculum	Medial side of fifth metacarpal
Intermediate muscles	Flexes each finger at metacarpo-phalangeal joints; extends each finger at interphalangeal joints	Fingers	Flexion	Lumbricals	Palm (lateral sides of tendons in flexor digitorum profundus)	Fingers 2–5 (lateral edges of extensional expansions on first phalanges)

TABLE 11.9

Muscle	Movement	Target	Target motion direction	Prime mover	Origin	Insertion
Intermediate muscles	Adducts and flexes each finger at metacarpo-phalangeal joints; extends each finger at interphalangeal joints	Fingers	Adduction; flexion; extension	Palmar interossei	Side of each metacarpal that faces metacarpal 3 (absent from metacarpal 3)	Extensor expansion on first phalanx of each finger (except finger 3) on side facing finger 3
Intermediate muscles	Abducts and flexes the three middle fingers at metacarpo-phalangeal joints; extends the three middle fingers at interphalangeal joints	Fingers	Abduction; flexion; extension	Dorsal interossei	Sides of metacarpals	Both sides of finger 3; for each other finger, extensor expansion over first phalanx on side opposite finger 3

TABLE 11.9

11.6 Appendicular Muscles of the Pelvic Girdle and Lower Limbs

LEARNING OBJECTIVES

By the end of this section, you will be able to:

- Identify the appendicular muscles of the pelvic girdle and lower limb
- Identify the movement and function of the pelvic girdle and lower limb

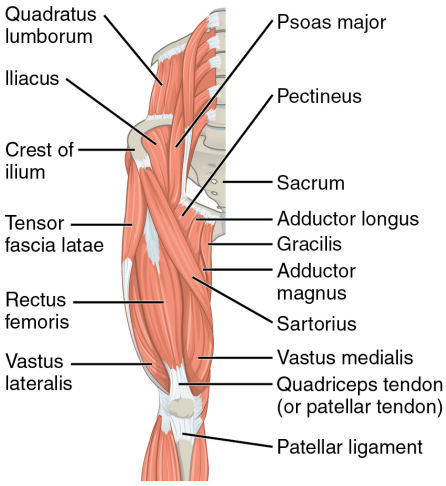
The appendicular muscles of the lower body position and stabilize the **pelvic girdle**, which serves as a foundation for the lower limbs. Comparatively, there is much more movement at the pectoral girdle than at the pelvic girdle. There is very little movement of the pelvic girdle because of its connection with the sacrum at the base of the axial skeleton. The pelvic girdle is less range of motion because it was designed to stabilize and support the body.

Muscles of the Thigh

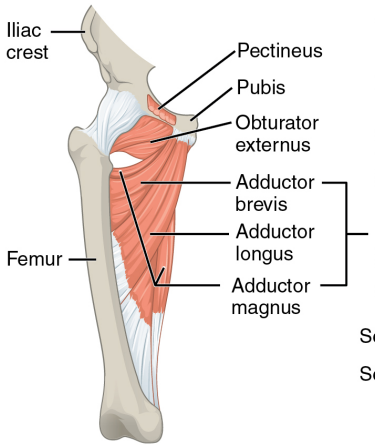
What would happen if the pelvic girdle, which attaches the lower limbs to the torso, were capable of the same range of motion as the pectoral girdle? For one thing, walking would expend more energy if the heads of the femurs were not secured in the acetabula of the pelvis. The body's center of gravity is in the area of the pelvis. If the center of gravity were not to remain fixed, standing up would be difficult as well. Therefore, what the leg muscles lack in range of motion and versatility, they make up for in size and power, facilitating the body's stabilization, posture, and movement.

Gluteal Region Muscles That Move the Femur

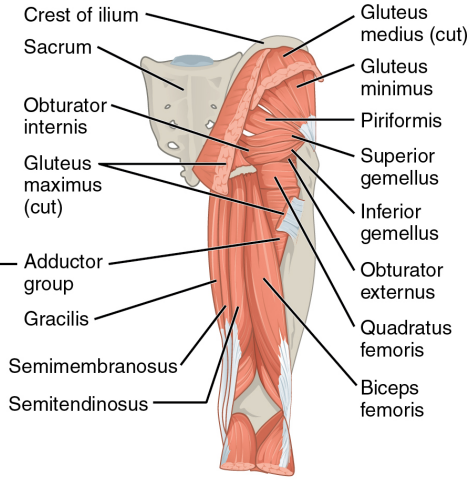
Most muscles that insert on the femur (the thigh bone) and move it, originate on the pelvic girdle. The **psoas major** and **iliacus** make up the **iliopsoas group**. Some of the largest and most powerful muscles in the body are the gluteal muscles or **gluteal group**. The **gluteus maximus** is the largest; deep to the gluteus maximus is the **gluteus medius**, and deep to the gluteus medius is the **gluteus minimus**, the smallest of the trio (Figure 11.29 and Figure 11.30).



Superficial pelvic and thigh muscles of right leg (anterior view)



Deep pelvic and thigh muscles of right leg (anterior view)



Pelvic and thigh muscles of right leg (posterior view)

FIGURE 11.29 Hip and Thigh Muscles The large and powerful muscles of the hip that move the femur generally originate on the pelvic girdle and insert into the femur. The muscles that move the lower leg typically originate on the femur and insert into the bones of the knee joint. The anterior muscles of the femur extend the lower leg but also aid in flexing the thigh. The posterior muscles of the femur flex the lower leg but also aid in extending the thigh. A combination of gluteal and thigh muscles also adduct, abduct, and rotate the thigh and lower leg.

Movement	Target	Target motion direction	Prime mover	Origin	Insertion
Iliopsoas group					
Raises knee at hip, as if performing a knee attack; assists lateral rotators in twisting thigh (and lower leg) outward; assists with bending over, maintaining posture	Femur	Thigh: flexion and lateral rotation; torso: flexion	Psoas major	Lumbar vertebrae (L1–L5); thoracic vertebra (T12)	Lesser trochanter of femur
Raises knee at hip, as if performing a knee attack; assists lateral rotators in twisting thigh (and lower leg) outward; assists with bending over, maintaining posture	Femur	Thigh: flexion and lateral rotation; torso: flexion	Iliacus	Iliac fossa; iliac crest; lateral sacrum	Lesser trochanter of femur
Gluteal group					
Lowers knee and moves thigh back, as when getting ready to kick a ball	Femur	Extension	Gluteus maximus	Dorsal ilium; sacrum; coccyx	Gluteal tuberosity of femur; iliotibial tract
Opens thighs, as when doing a split	Femur	Abduction	Gluteus medius	Lateral surface of ilium	Greater trochanter of femur
Brings the thighs back together	Femur	Abduction	Gluteus minimus	External surface of ilium	Greater trochanter of femur
Assists with raising knee at hip and opening thighs; maintains posture by stabilizing the iliotibial track, which connects to the knee	Femur	Flexion; abduction	Tensor fascia lata	Anterior aspect of iliac crest; anterior superior iliac spine	Iliotibial tract
Lateral rotators					
Twists thigh (and lower leg) outward; maintains posture by stabilizing hip joint	Femur	Lateral rotation	Piriformis	Anterolateral surface of sacrum	Greater trochanter of femur
Twists thigh (and lower leg) outward; maintains posture by stabilizing hip joint	Femur	Lateral rotation	Obutrator internus	Inner surface of obturator membrane; greater sciatic notch; margins of obturator foramen	Greater trochanter in front of piriformis
Twists thigh (and lower leg) outward; maintains posture by stabilizing hip joint	Femur	Lateral rotation	Obturator externus	Outer surfaces of obturator membrane, pubic, and ischium; margins of obturator foramen	Trochanteric fossa of posterior femur
Twists thigh (and lower leg) outward; maintains posture by stabilizing hip joint	Femur	Lateral rotation	Superior gemellus	Ischial spine	Greater trochanter of femur
Twists thigh (and lower leg) outward; maintains posture by stabilizing hip joint	Femur	Lateral rotation	Inferior gemellus	Ischial tuberosity	Greater trochanter of femur
Twists thigh (and lower leg) outward; maintains posture by stabilizing hip joint	Femur	Lateral rotation	Quadratus femoris	Ischial tuberosity	Trochanteric crest of femur
Adductors					
Brings the thighs back together; assists with raising the knee	Femur	Adduction; flexion	Adductor longus	Pubis near pubic symphysis	Linea aspera
Brings the thighs back together; assists with raising the knee	Femur	Adduction; flexion	Adductor brevis	Body of pubis; inferior ramus of pubis	Linea aspera above adductor longus
Brings the thighs back together; assists with raising the knee and moving the thigh back	Femur	Adduction; flexion; extension	Adductor magnus	Ischial rami; pubic rami; ischial tuberosity	Linea aspera; adductor tubercle of femur
Opens thighs; assists with raising the knee and turning the thigh (and lower leg) inward	Femur	Adduction; flexion; medial rotation	Pectineus	Pectineal line of pubis	Lesser trochanter to linea aspera of posterior aspect of femur

FIGURE 11.30 **Gluteal Region Muscles That Move the Femur**

The **tensor fascia latae** is a thick, squarish muscle in the superior aspect of the lateral thigh. It acts as a synergist of the gluteus medius and iliopsoas in flexing and abducting the thigh. It also helps stabilize the lateral aspect of the

knee by pulling on the **iliotibial tract** (band), making it taut. Deep to the gluteus maximus, the **piriformis**, **obturator internus**, **obturator externus**, **superior gemellus**, **inferior gemellus**, and **quadratus femoris** laterally rotate the femur at the hip.

The **adductor longus**, **adductor brevis**, and **adductor magnus** can both medially and laterally rotate the thigh depending on the placement of the foot. The adductor longus flexes the thigh, whereas the adductor magnus extends it. The **pectineus** adducts and flexes the femur at the hip as well. The pectineus is located in the **femoral triangle**, which is formed at the junction between the hip and the leg and also includes the femoral nerve, the femoral artery, the femoral vein, and the deep inguinal lymph nodes.

Thigh Muscles That Move the Femur, Tibia, and Fibula

Deep fascia in the thigh separates it into medial, anterior, and posterior compartments (see Figure 11.29 and Figure 11.31). The muscles in the **medial compartment of the thigh** are responsible for adducting the femur at the hip. Along with the adductor longus, adductor brevis, adductor magnus, and pectineus, the strap-like **gracilis** adducts the thigh in addition to flexing the leg at the knee.

Movement	Target	Target motion direction	Prime mover	Origin	Insertion
Medial compartment of thigh					
Moves back of lower legs up toward buttocks, as when kneeling; assists in opening thighs	Femur; tibia/fibula	Tibia/fibula: flexion; thigh: adduction	Gracilis	Inferior ramus; body of pubis; ischial ramus	Medial surface of tibia
Anterior compartment of thigh: Quadriceps femoris group					
Moves lower leg out in front of body, as when kicking; assists in raising the knee	Femur; tibia/fibula	Tibia/fibula: extension; thigh: flexion	Rectus femoris	Anterior inferior iliac spine; superior margin of acetabulum	Patella; tibial tuberosity
Moves lower leg out in front of body, as when kicking	Tibia/fibula	Extension	Vastus lateralis	Greater trochanter; intertrochanteric line; linea aspera	Patella; tibial tuberosity
Moves lower leg out in front of body, as when kicking	Tibia/fibula	Extension	Vastus medialis	Linea aspera; intertrochanteric line	Patella; tibial tuberosity
Moves lower leg out in front of body, as when kicking	Tibia/fibula	Extension	Vastus intermedius	Proximal femur shaft	Patella; tibial tuberosity
Moves back of lower legs up and back toward the buttocks, as when kneeling; assists in moving thigh diagonally upward and outward as when mounting a bike	Femur; tibia/fibula	Tibia: flexion; thigh: flexion, abduction, lateral rotation	Sartorius	Anterior superior iliac spine	Medial aspect of proximal tibia
Posterior compartment of thigh: Hamstring group					
Moves back of lower legs up and back toward the buttocks, as when kneeling; moves thigh down and back; twists the thigh (and lower leg) outward	Femur; tibia/fibula	Tibia/fibula: flexion; thigh: extension, lateral rotation	Biceps femoris	Ischial tuberosity; linea aspera; distal femur	Head of fibula; lateral condyle of tibia
Moves back of lower legs up toward buttocks, as when kneeling; moves thigh down and back; twists the thigh (and lower leg) inward	Femur; tibia/fibula	Tibia/fibula: flexion; thigh: extension, medial rotation	Semitendinosus	Ischial tuberosity	Upper tibial shaft
Moves back of lower legs up and back toward the buttocks as when kneeling; moves thigh down and back; twists the thigh (and lower leg) inward	Femur; tibia/fibula	Tibia/fibula: flexion; thigh: extension, medial rotation	Semi-membranosus	Ischial tuberosity	Medial condyle of tibia; lateral condyle of femur

FIGURE 11.31 **Thigh Muscles That Move the Femur, Tibia, and Fibula**

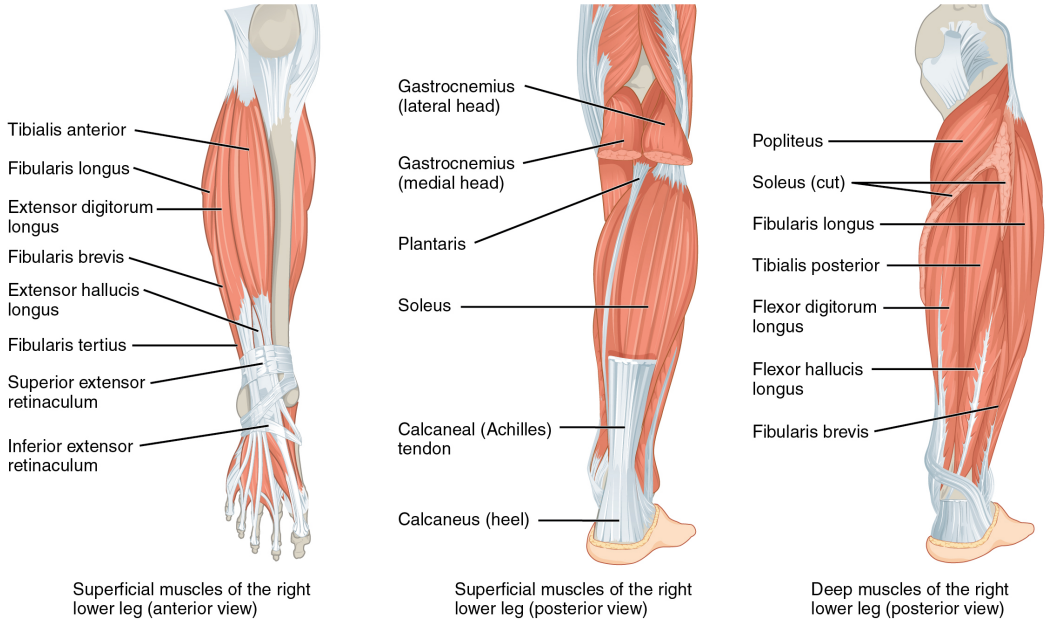
The muscles of the **anterior compartment of the thigh** flex the thigh and extend the leg. This compartment contains the **quadriceps femoris group**, which actually comprises four muscles that extend and stabilize the knee. The **rectus femoris** is on the anterior aspect of the thigh, the **vastus lateralis** is on the lateral aspect of the thigh, the **vastus medialis** is on the medial aspect of the thigh, and the **vastus intermedius** is between the vastus lateralis and vastus medialis and deep to the rectus femoris. The tendon common to all four is the **quadriceps tendon** (patellar tendon), which inserts into the patella and continues below it as the **patellar ligament**. The patellar ligament attaches to the tibial tuberosity. In addition to the quadriceps femoris, the **sartorius** is a band-like muscle that extends from the anterior superior iliac spine to the medial side of the proximal tibia. This versatile muscle flexes the leg at the knee and flexes, abducts, and laterally rotates the leg at the hip. This muscle allows us to sit

cross-legged.

The **posterior compartment of the thigh** includes muscles that flex the leg and extend the thigh. The three long muscles on the back of the knee are the **hamstring group**, which flexes the knee. These are the **biceps femoris**, **semitendinosus**, and **semimembranosus**. The tendons of these muscles form the **popliteal fossa**, the diamond-shaped space at the back of the knee.

Muscles That Move the Feet and Toes

Similar to the thigh muscles, the muscles of the leg are divided by deep fascia into compartments, although the leg has three: anterior, lateral, and posterior (Figure 11.32 and Figure 11.33).



Superficial muscles of the right lower leg (anterior view)

Superficial muscles of the right lower leg (posterior view)

Deep muscles of the right lower leg (posterior view)

FIGURE 11.32 Muscles of the Lower Leg The muscles of the anterior compartment of the lower leg are generally responsible for dorsiflexion, and the muscles of the posterior compartment of the lower leg are generally responsible for plantar flexion. The lateral and medial muscles in both compartments invert, evert, and rotate the foot.

Movement	Target	Target motion direction	Prime mover	Origin	Insertion
Anterior compartment of leg					
Raises the sole of the foot off the ground, as when preparing to foot-tap; bends the inside of the foot upwards, as when catching your balance while falling laterally toward the opposite side as the balancing foot	Foot	Dorsiflexion; inversion	Tibialis anterior	Lateral condyle and upper tibial shaft; interosseous membrane	Interior surface of medial cuneiform; First metatarsal bone
Raises the sole of the foot off the ground, as when preparing to foot-tap; extends the big toe	Foot; big toe	Foot: dorsiflexion; big toe: extension	Extensor hallucis longus	Anteromedial fibula shaft; interosseous membrane	Distal phalanx of big toe
Raises the sole of the foot off the ground, as when preparing to foot-tap; extends toes	Foot; toes 2–5	Foot: dorsiflexion; toes: extension	Extensor digitorum longus	Lateral condyle of tibia; proximal portion of fibula; interosseous membrane	Middle and distal phalanges of toes 2–5
Lateral compartment of leg					
Lowers the sole of the foot to the ground, as when foot-tapping or jumping; bends the inside of the foot downwards, as when catching your balance while falling laterally toward the same side as the balancing foot	Foot	Plantar flexion and eversion	Fibularis longus	Upper portion of lateral fibula	First metatarsal; medial cuneiform
Lowers the sole of the foot to the ground, as when foot-tapping or jumping; bends the inside of the foot downward, as when catching your balance while falling laterally toward the same side as the balancing foot	Foot	Plantar flexion and eversion	Fibularis (peroneus) brevis	Distal fibula shaft	Proximal end of fifth metatarsal
Posterior compartment of leg: Superficial muscles					
Lowers the sole of the foot to the ground, as when foot-tapping or jumping; assists in moving the back of the lower legs up and back toward the buttocks	Foot; tibia/ fibula	Foot: plantar flexion; tibia/fibula: flexion	Gastrocnemius	Medial and lateral condyles of femur	Posterior calcaneus
Lowers the sole of the foot to the ground, as when foot-tapping or jumping; maintains posture while walking	Foot	Plantar flexion	Soleus	Superior tibia; fibula; interosseous membrane	Posterior calcaneus
Lowers the sole of the foot to the ground, as when foot-tapping or jumping; assists in moving the back of the lower legs up and back toward the buttocks	Foot; tibia/ fibula	Foot: plantar flexion; tibia/fibula: flexion	Plantaris	Posterior femur above lateral condyle	Calcaneus or calcaneus tendon
Lowers the sole of the foot to the ground, as when foot-tapping or jumping	Foot	Plantar flexion	Tibialis posterior	Superior tibia and fibula; interosseous membrane	Several tarsals and metatarsals 2–4
Posterior compartment of leg: Deep muscles					
Moves the back of the lower legs up and back toward the buttocks; assists in rotation of the leg at the knee and thigh	Tibia/ fibula	Tibia/fibula: flexion thigh and lower leg: medial and lateral rotation	Popliteus	Lateral condyle of femur; lateral meniscus	Proximal tibia
Lowers the sole of the foot to the ground, as when foot-tapping or jumping; bends the inside of the foot upward and flexes toes	Foot; toes 2–5	Foot: plantar flexion and inversion toes: flexion	Flexor digitorum longus	Posterior tibia	Distal phalanges of toes 2–5
Flexes the big toe	Big toe; foot	Big toe: flexion foot: plantar flexion	Flexor hallucis longus	Midshaft of fibula; interosseous membrane	Distal phalanx of big toe

FIGURE 11.33 **Muscles That Move the Feet and Toes**

The muscles in the **anterior compartment of the leg**: the **tibialis anterior**, a long and thick muscle on the lateral surface of the tibia, the **extensor hallucis longus**, deep under it, and the **extensor digitorum longus**, lateral to it, all contribute to raising the front of the foot when they contract. The **fibularis tertius**, a small muscle that originates on the anterior surface of the fibula, is associated with the extensor digitorum longus and sometimes fused to it, but is not present in all people. Thick bands of connective tissue called the **superior extensor retinaculum** (transverse ligament of the ankle) and the **inferior extensor retinaculum**, hold the tendons of these muscles in place during dorsiflexion.

The **lateral compartment of the leg** includes two muscles: the **fibularis longus** (peroneus longus) and the **fibularis brevis** (peroneus brevis). The superficial muscles in the **posterior compartment of the leg** all insert onto the **calcaneal tendon** (Achilles tendon), a strong tendon that inserts into the calcaneal bone of the ankle. The muscles in this compartment are large and strong and keep humans upright. The most superficial and visible muscle of the calf is the **gastrocnemius**. Deep to the gastrocnemius is the wide, flat **soleus**. The **plantaris** runs obliquely between the two; some people may have two of these muscles, whereas no plantaris is observed in about seven percent of other cadaver dissections. The plantaris tendon is a desirable substitute for the fascia lata in hernia repair, tendon transplants, and repair of ligaments. There are four deep muscles in the posterior compartment of the leg as well: the **popliteus**, **flexor digitorum longus**, **flexor hallucis longus**, and **tibialis posterior**.

The foot also has intrinsic muscles, which originate and insert within it (similar to the intrinsic muscles of the hand). These muscles primarily provide support for the foot and its arch, and contribute to movements of the toes (Figure 11.34 and Figure 11.35). The principal support for the longitudinal arch of the foot is a deep fascia called **plantar aponeurosis**, which runs from the calcaneus bone to the toes (inflammation of this tissue is the cause of "plantar fasciitis," which can affect runners. The intrinsic muscles of the foot consist of two groups. The **dorsal group** includes only one muscle, the **extensor digitorum brevis**. The second group is the **plantar group**, which consists of four layers, starting with the most superficial.

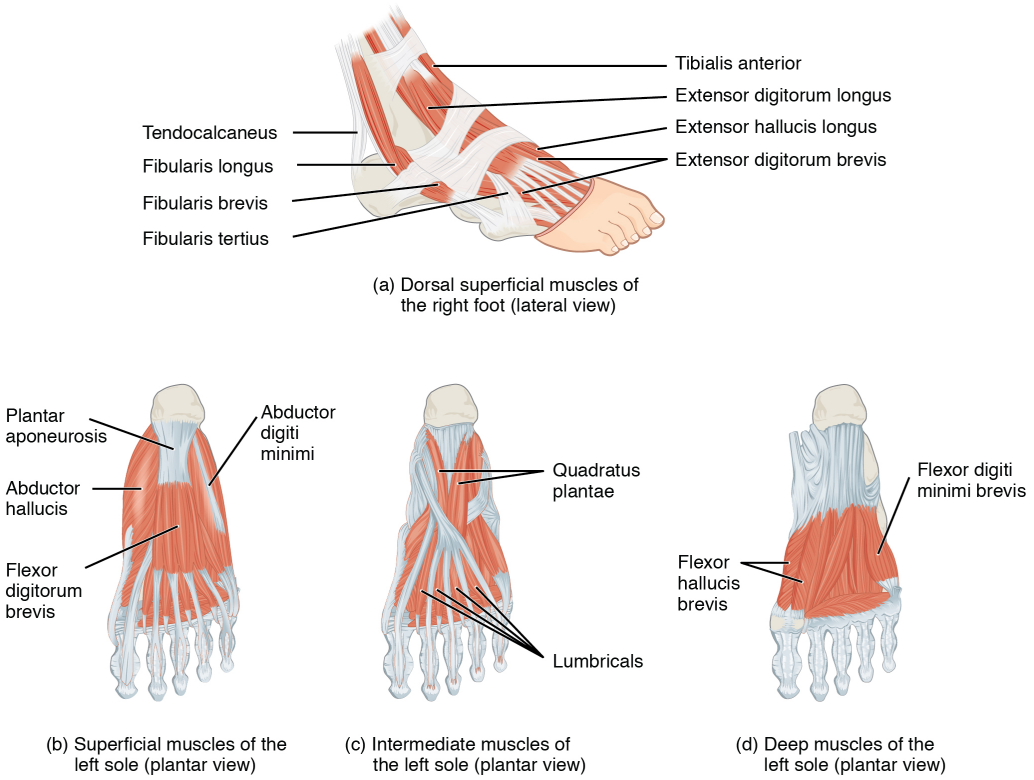


FIGURE 11.34 Intrinsic Muscles of the Foot The muscles along the dorsal side of the foot (a) generally extend the toes while the muscles of the plantar side of the foot (b, c, d) generally flex the toes. The plantar muscles exist in three layers, providing the foot the strength to counterbalance the weight of the body. In this diagram, these three layers are shown from a plantar view beginning with the bottom-most layer just under the plantar skin of the foot (b) and ending with the top-most layer (d) located just inferior to the foot and toe bones.

Movement	Target	Target motion direction	Prime mover	Origin	Insertion
Dorsal group					
Extends toes 2–5	Toes 2–5	Extension	Extensor digitorum brevis	Calcaneus; extensor retinaculum	Base of proximal phalanx of big toe; extensor expansions on toes 2–5
Plantar group (layer 1)					
Abducts and flexes big toe	Big toe	Adduction; flexion	Abductor hallucis	Calcaneal tuberosity; flexor retinaculum	Proximal phalanx of big toe
Flexes toes 2–4	Middle toes	Flexion	Flexor digitorum brevis	Calcaneal tuberosity	Middle phalanx of toes 2–4
Abducts and flexes small toe	Toe 5	Abduction; flexion	Abductor digiti minimi	Calcaneal tuberosity	Proximal phalanx of little toe
Plantar group (layer 2)					
Assists in flexing toes 2–5	Toes 2–5	Flexion	Quadratus plantae	Medial and lateral sides of calcaneus	Tendon of flexor digitorum longus
Extends toes 2–5 at the interphalangeal joints; flexes the small toes at the metatarsophalangeal joints	Toes 2–5	Extension; flexion	Lumbricals	Tendons of flexor digitorum longus	Medial side of proximal phalanx of toes 2–5
Plantar group (layer 3)					
Flexes big toe	Big toe	Flexion	Flexor hallucis brevis	Lateral cuneiform; cuboid bones	Base of proximal phalanx of big toe
Adducts and flexes big toe	Big toe	Adduction; flexion	Adductor hallucis	Bases of metatarsals 2–4; fibularis longus tendon sheath; ligament across metatarsophalangeal joints	Base of proximal phalanx of big toe
Flexes small toe	Little toe	Flexion	Flexor digiti minimi brevis	Base of metatarsal 5; tendon sheath of fibularis longus	Base of proximal phalanx of little toe
Plantar group (layer 4)					
Abducts and flexes middle toes at metatarsophalangeal joints; extends middle toes at interphalangeal joints	Middle toes	Abduction; flexion; extension	Dorsal interossei	Sides of metatarsals	Both sides of toe 2; for each other toe, extensor expansion over first phalanx on side opposite toe 2
Abducts toes 3–5; flexes proximal phalanges and extends distal phalanges	Small toes	Abduction; flexion; extension	Plantar interossei	Side of each metatarsal that faces metatarsal 2 (absent from metatarsal 2)	Extensor expansion on first phalanx of each toe (except to 2) on side facing toe 2

FIGURE 11.35 **Intrinsic Muscles in the Foot**

Key Terms

abduct move away from midline in the sagittal plane
abductor moves the bone away from the midline
abductor digiti minimi muscle that abducts the little finger
abductor pollicis brevis muscle that abducts the thumb
abductor pollicis longus muscle that inserts into the first metacarpal
adductor moves the bone toward the midline
adductor brevis muscle that adducts and medially rotates the thigh
adductor longus muscle that adducts, medially rotates, and flexes the thigh
adductor magnus muscle with an anterior fascicle that adducts, medially rotates and flexes the thigh, and a posterior fascicle that assists in thigh extension
adductor pollicis muscle that adducts the thumb
agonist (also, prime mover) muscle whose contraction is responsible for producing a particular motion
anal triangle posterior triangle of the perineum that includes the anus
anconeus small muscle on the lateral posterior elbow that extends the forearm
antagonist muscle that opposes the action of an agonist
anterior compartment of the arm (anterior flexor compartment of the arm) the biceps brachii, brachialis, brachioradialis, and their associated blood vessels and nerves
anterior compartment of the forearm (anterior flexor compartment of the forearm) deep and superficial muscles that originate on the humerus and insert into the hand
anterior compartment of the leg region that includes muscles that dorsiflex the foot
anterior compartment of the thigh region that includes muscles that flex the thigh and extend the leg
anterior scalene a muscle anterior to the middle scalene
appendicular of the arms and legs
axial of the trunk and head
belly bulky central body of a muscle
bi two
biceps brachii two-headed muscle that crosses the shoulder and elbow joints to flex the forearm while assisting in supinating it and flexing the arm at the shoulder
biceps femoris hamstring muscle
bipennate pennate muscle that has fascicles that are located on both sides of the tendon
brachialis muscle deep to the biceps brachii that provides power in flexing the forearm.
brachioradialis muscle that can flex the forearm quickly or help lift a load slowly
brevis short
buccinator muscle that compresses the cheek
calcaneal tendon (also, Achilles tendon) strong tendon that inserts into the calcaneal bone of the ankle
caval opening opening in the diaphragm that allows the inferior vena cava to pass through; foramen for the vena cava
circular (also, sphincter) fascicles that are concentrically arranged around an opening
compressor urethrae deep perineal muscle in females
convergent fascicles that extend over a broad area and converge on a common attachment site
coracobrachialis muscle that flexes and adducts the arm
corrugator supercilii prime mover of the eyebrows
deep anterior compartment flexor pollicis longus, flexor digitorum profundus, and their associated blood vessels and nerves
deep posterior compartment of the forearm (deep posterior extensor compartment of the forearm) the abductor pollicis longus, extensor pollicis brevis, extensor pollicis longus, extensor indicis, and their associated blood vessels and nerves
deep transverse perineal deep perineal muscle in males
deglutition swallowing
deltoid shoulder muscle that abducts the arm as well as flexes and medially rotates it, and extends and laterally rotates it
diaphragm skeletal muscle that separates the thoracic and abdominal cavities and is dome-shaped at rest
digastric muscle that has anterior and posterior bellies and elevates the hyoid bone and larynx when one swallows; it also depresses the mandible
dorsal group region that includes the extensor digitorum brevis
dorsal interossei muscles that abduct and flex the three middle fingers at the metacarpophalangeal joints and extend them at the interphalangeal joints
epicranial aponeurosis (also, galea aponeurosis) flat broad tendon that connects the frontalis and occipitalis
erector spinae group large muscle mass of the back; primary extensor of the vertebral column

extensor muscle that increases the angle at the joint
extensor carpi radialis brevis muscle that extends and abducts the hand at the wrist
extensor carpi ulnaris muscle that extends and adducts the hand
extensor digiti minimi muscle that extends the little finger
extensor digitorum muscle that extends the hand at the wrist and the phalanges
extensor digitorum brevis muscle that extends the toes
extensor digitorum longus muscle that is lateral to the tibialis anterior
extensor hallucis longus muscle that is partly deep to the tibialis anterior and extensor digitorum longus
extensor indicis muscle that inserts onto the tendon of the extensor digitorum of the index finger
extensor pollicis brevis muscle that inserts onto the base of the proximal phalanx of the thumb
extensor pollicis longus muscle that inserts onto the base of the distal phalanx of the thumb
extensor radialis longus muscle that extends and abducts the hand at the wrist
extensor retinaculum band of connective tissue that extends over the dorsal surface of the hand
external intercostal superficial intercostal muscles that raise the rib cage
external oblique superficial abdominal muscle with fascicles that extend inferiorly and medially
extrinsic eye muscles originate outside the eye and insert onto the outer surface of the white of the eye, and create eyeball movement
extrinsic muscles of the hand muscles that move the wrists, hands, and fingers and originate on the arm
fascicle muscle fibers bundled by perimysium into a unit
femoral triangle region formed at the junction between the hip and the leg and includes the pectineus, femoral nerve, femoral artery, femoral vein, and deep inguinal lymph nodes
fibularis brevis (also, peroneus brevis) muscle that plantar flexes the foot at the ankle and everts it at the intertarsal joints
fibularis longus (also, peroneus longus) muscle that plantar flexes the foot at the ankle and everts it at the intertarsal joints
fibularis tertius small muscle that is associated with the extensor digitorum longus
fixator synergist that assists an agonist by preventing or reducing movement at another joint, thereby stabilizing the origin of the agonist
flexion movement that decreases the angle of a joint
flexor muscle that decreases the angle at the joint
flexor carpi radialis muscle that flexes and abducts the hand at the wrist
flexor carpi ulnaris muscle that flexes and adducts the hand at the wrist
flexor digiti minimi brevis muscle that flexes the little finger
flexor digitorum longus muscle that flexes the four small toes
flexor digitorum profundus muscle that flexes the phalanges of the fingers and the hand at the wrist
flexor digitorum superficialis muscle that flexes the hand and the digits
flexor hallucis longus muscle that flexes the big toe
flexor pollicis brevis muscle that flexes the thumb
flexor pollicis longus muscle that flexes the distal phalanx of the thumb
flexor retinaculum band of connective tissue that extends over the palmar surface of the hand
frontalis front part of the occipitofrontalis muscle
fusiform muscle that has fascicles that are spindle-shaped to create large bellies
gastrocnemius most superficial muscle of the calf
genioglossus muscle that originates on the mandible and allows the tongue to move downward and forward
geniohyoid muscle that depresses the mandible, and raises and pulls the hyoid bone anteriorly
gluteal group muscle group that extends, flexes, rotates, adducts, and abducts the femur
gluteus maximus largest of the gluteus muscles that extends the femur
gluteus medius muscle deep to the gluteus maximus that abducts the femur at the hip
gluteus minimus smallest of the gluteal muscles and deep to the gluteus medius
gracilis muscle that adducts the thigh and flexes the leg at the knee
hamstring group three long muscles on the back of the leg
hyoglossus muscle that originates on the hyoid bone to move the tongue downward and flatten it
hypothenar group of muscles on the medial aspect of the palm
hypothenar eminence rounded contour of muscle at the base of the little finger
iliacus muscle that, along with the psoas major, makes up the iliopsoas
iliococcygeus muscle that makes up the levator ani along with the pubococcygeus
iliocostalis cervicis muscle of the iliocostalis group associated with the cervical region
iliocostalis group laterally placed muscles of the

erector spinae

iliocostalis lumborum muscle of the iliocostalis group associated with the lumbar region

iliocostalis thoracis muscle of the iliocostalis group associated with the thoracic region

iliopsoas group muscle group consisting of iliacus and psoas major muscles, that flexes the thigh at the hip, rotates it laterally, and flexes the trunk of the body onto the hip

iliotibial tract muscle that inserts onto the tibia; made up of the gluteus maximus and connective tissues of the tensor fasciae latae

inferior extensor retinaculum cruciate ligament of the ankle

inferior gemellus muscle deep to the gluteus maximus on the lateral surface of the thigh that laterally rotates the femur at the hip

infrahyoid muscles anterior neck muscles that are attached to, and inferior to the hyoid bone

infraspinatus muscle that laterally rotates the arm

innermost intercostal the deepest intercostal muscles that draw the ribs together

insertion end of a skeletal muscle that is attached to the structure (usually a bone) that is moved when the muscle contracts

intercostal muscles muscles that span the spaces between the ribs

intermediate group of midpalmar muscles

internal intercostal muscles the intermediate intercostal muscles that draw the ribs together

internal oblique flat, intermediate abdominal muscle with fascicles that run perpendicular to those of the external oblique

intrinsic muscles of the hand muscles that move the wrists, hands, and fingers and originate in the palm

ischiococcygeus muscle that assists the levator ani and pulls the coccyx anteriorly

lateral compartment of the leg region that includes the fibularis (peroneus) longus and the fibularis (peroneus) brevis and their associated blood vessels and nerves

lateral pterygoid muscle that moves the mandible from side to side

lateralis to the outside

latissimus dorsi broad, triangular axial muscle located on the inferior part of the back

levator ani pelvic muscle that resists intra-abdominal pressure and supports the pelvic viscera

linea alba white, fibrous band that runs along the midline of the trunk

longissimus capitis muscle of the longissimus group associated with the head region

longissimus cervicis muscle of the longissimus group associated with the cervical region

longissimus group intermediately placed muscles of the erector spinae

longissimus thoracis muscle of the longissimus group associated with the thoracic region

longus long

lumbrical muscle that flexes each finger at the metacarpophalangeal joints and extend each finger at the interphalangeal joints

masseter main muscle for chewing that elevates the mandible to close the mouth

mastication chewing

maximus largest

medial compartment of the thigh a region that includes the adductor longus, adductor brevis, adductor magnus, pectineus, gracilis, and their associated blood vessels and nerves

medial pterygoid muscle that moves the mandible from side to side

medialis to the inside

medius medium

middle scalene longest scalene muscle, located between the anterior and posterior scalenes

minimus smallest

multifidus muscle of the lumbar region that helps extend and laterally flex the vertebral column

multipennate pennate muscle that has a tendon branching within it

mylohyoid muscle that lifts the hyoid bone and helps press the tongue to the top of the mouth

oblique at an angle

obturator externus muscle deep to the gluteus maximus on the lateral surface of the thigh that laterally rotates the femur at the hip

obturator internus muscle deep to the gluteus maximus on the lateral surface of the thigh that laterally rotates the femur at the hip

occipitalis posterior part of the occipitofrontalis muscle

occipitofrontalis muscle that makes up the scalp with a frontal belly and an occipital belly

omohyoid muscle that has superior and inferior bellies and depresses the hyoid bone

opponens digiti minimi muscle that brings the little finger across the palm to meet the thumb

opponens pollicis muscle that moves the thumb across the palm to meet another finger

orbicularis oculi circular muscle that closes the eye

orbicularis oris circular muscle that moves the lips

origin end of a skeletal muscle that is attached to another structure (usually a bone) in a fixed position

palatoglossus muscle that originates on the soft palate to elevate the back of the tongue

palmar interossei muscles that abduct and flex each finger at the metacarpophalangeal joints and extend each finger at the interphalangeal joints
palmaris longus muscle that provides weak flexion of the hand at the wrist
parallel fascicles that extend in the same direction as the long axis of the muscle
patellar ligament extension of the quadriceps tendon below the patella
pectineus muscle that abducts and flexes the femur at the hip
pectoral girdle shoulder girdle, made up of the clavicle and scapula
pectoralis major thick, fan-shaped axial muscle that covers much of the superior thorax
pectoralis minor muscle that moves the scapula and assists in inhalation
pelvic diaphragm muscular sheet that comprises the levator ani and the ischiococcygeus
pelvic girdle hips, a foundation for the lower limb
pennate fascicles that are arranged differently based on their angles to the tendon
perineum diamond-shaped region between the pubic symphysis, coccyx, and ischial tuberosities
piriformis muscle deep to the gluteus maximus on the lateral surface of the thigh that laterally rotates the femur at the hip
plantar aponeurosis muscle that supports the longitudinal arch of the foot
plantar group four-layered group of intrinsic foot muscles
plantaris muscle that runs obliquely between the gastrocnemius and the soleus
popliteal fossa diamond-shaped space at the back of the knee
popliteus muscle that flexes the leg at the knee and creates the floor of the popliteal fossa
posterior compartment of the leg region that includes the superficial gastrocnemius, soleus, and plantaris, and the deep popliteus, flexor digitorum longus, flexor hallucis longus, and tibialis posterior
posterior compartment of the thigh region that includes muscles that flex the leg and extend the thigh
posterior scalene smallest scalene muscle, located posterior to the middle scalene
prime mover (also, agonist) principle muscle involved in an action
pronator quadratus pronator that originates on the ulna and inserts on the radius
pronator teres pronator that originates on the humerus and inserts on the radius
psoas major muscle that, along with the iliacus, makes up the iliopsoas
pubococcygeus muscle that makes up the levator ani along with the iliococcygeus
quadratus femoris muscle deep to the gluteus maximus on the lateral surface of the thigh that laterally rotates the femur at the hip
quadratus lumborum posterior part of the abdominal wall that helps with posture and stabilization of the body
quadriceps femoris group four muscles, that extend and stabilize the knee
quadriceps tendon (also, patellar tendon) tendon common to all four quadriceps muscles, inserts into the patella
rectus straight
rectus abdominis long, linear muscle that extends along the middle of the trunk
rectus femoris quadricep muscle on the anterior aspect of the thigh
rectus sheaths tissue that makes up the linea alba
retinacula fibrous bands that sheath the tendons at the wrist
rhomboid major muscle that attaches the vertebral border of the scapula to the spinous process of the thoracic vertebrae
rhomboid minor muscle that attaches the vertebral border of the scapula to the spinous process of the thoracic vertebrae
rotator cuff (also, musculotendinous cuff) the circle of tendons around the shoulder joint
sartorius band-like muscle that flexes, abducts, and laterally rotates the leg at the hip
scalene muscles flex, laterally flex, and rotate the head; contribute to deep inhalation
segmental muscle group interspinales and intertransversarii muscles that bring together the spinous and transverse processes of each consecutive vertebra
semimembranosus hamstring muscle
semispinalis capitis transversospinales muscle associated with the head region
semispinalis cervicis transversospinales muscle associated with the cervical region
semispinalis thoracis transversospinales muscle associated with the thoracic region
semitendinosus hamstring muscle
serratus anterior large and flat muscle that originates on the ribs and inserts onto the scapula
soleus wide, flat muscle deep to the gastrocnemius
sphincter urethrovaginalis deep perineal muscle in females
spinalis capitis muscle of the spinalis group associated with the head region

spinalis cervicis muscle of the spinalis group associated with the cervical region
spinalis group medially placed muscles of the erector spinae
spinalis thoracis muscle of the spinalis group associated with the thoracic region
splenius posterior neck muscles; includes the splenius capitis and splenius cervicis
splenius capitis neck muscle that inserts into the head region
splenius cervicis neck muscle that inserts into the cervical region
sternocleidomastoid major muscle that laterally flexes and rotates the head
sternohyoid muscle that depresses the hyoid bone
sternothyroid muscle that depresses the larynx's thyroid cartilage
styloglossus muscle that originates on the styloid bone, and allows upward and backward motion of the tongue
stylohyoid muscle that elevates the hyoid bone posteriorly
subclavius muscle that stabilizes the clavicle during movement
subscapularis muscle that originates on the anterior scapula and medially rotates the arm
superficial anterior compartment of the forearm flexor carpi radialis, palmaris longus, flexor carpi ulnaris, flexor digitorum superficialis, and their associated blood vessels and nerves
superficial posterior compartment of the forearm extensor radialis longus, extensor carpi radialis brevis, extensor digitorum, extensor digiti minimi, extensor carpi ulnaris, and their associated blood vessels and nerves
superior extensor retinaculum transverse ligament of the ankle
superior gemellus muscle deep to the gluteus maximus on the lateral surface of the thigh that laterally rotates the femur at the hip
supinator muscle that moves the palm and forearm anteriorly
suprahyoid muscles neck muscles that are superior to the hyoid bone
supraspinatus muscle that abducts the arm
synergist muscle whose contraction helps a prime mover in an action
temporalis muscle that retracts the mandible
tendinous intersections three transverse bands of collagen fibers that divide the rectus abdominis into segments
tensor fascia lata muscle that flexes and abducts the thigh
teres major muscle that extends the arm and assists in adduction and medial rotation of it
teres minor muscle that laterally rotates and extends the arm
thenar group of muscles on the lateral aspect of the palm
thenar eminence rounded contour of muscle at the base of the thumb
thyrohyoid muscle that depresses the hyoid bone and elevates the larynx's thyroid cartilage
tibialis anterior muscle located on the lateral surface of the tibia
tibialis posterior muscle that plantar flexes and inverts the foot
transversospinales muscles that originate at the transverse processes and insert at the spinous processes of the vertebrae
transversus abdominis deep layer of the abdomen that has fascicles arranged transversely around the abdomen
trapezius muscle that stabilizes the upper part of the back
tri three
triceps brachii three-headed muscle that extends the forearm
unipennate pennate muscle that has fascicles located on one side of the tendon
urogenital triangle anterior triangle of the perineum that includes the external genitals
vastus intermedius quadricep muscle that is between the vastus lateralis and vastus medialis and is deep to the rectus femoris
vastus lateralis quadricep muscle on the lateral aspect of the thigh
vastus medialis quadricep muscle on the medial aspect of the thigh

Chapter Review

11.1 Interactions of Skeletal Muscles, Their Fascicle Arrangement, and Their Lever Systems

Skeletal muscles each have an origin and an insertion. The end of the muscle that attaches to the bone being pulled is called the muscle's insertion and the end of the muscle attached to a fixed, or stabilized, bone is called the origin. The muscle primarily responsible for a movement is called the prime mover, and muscles that assist in this action are called synergists. A synergist that makes the insertion site more stable is

called a fixator. Meanwhile, a muscle with the opposite action of the prime mover is called an antagonist. Several factors contribute to the force generated by a skeletal muscle. One is the arrangement of the fascicles in the skeletal muscle. Fascicles can be parallel, circular, convergent, pennate, fusiform, or triangular. Each arrangement has its own range of motion and ability to do work.

11.2 Naming Skeletal Muscles

Muscle names are based on many characteristics. The location of a muscle in the body is important. Some muscles are named based on their size and location, such as the gluteal muscles of the buttocks. Other muscle names can indicate the location in the body or bones with which the muscle is associated, such as the tibialis anterior. The shapes of some muscles are distinctive; for example, the direction of the muscle fibers is used to describe muscles of the body midline. The origin and/or insertion can also be features used to name a muscle; examples are the biceps brachii, triceps brachii, and the pectoralis major.

11.3 Axial Muscles of the Head, Neck, and Back

Muscles are either axial muscles or appendicular. The axial muscles are grouped based on location, function, or both. Some axial muscles cross over to the appendicular skeleton. The muscles of the head and neck are all axial. The muscles in the face create facial expression by inserting into the skin rather than onto bone. Muscles that move the eyeballs are extrinsic, meaning they originate outside of the eye and insert onto it. Tongue muscles are both extrinsic and intrinsic. The genioglossus depresses the tongue and moves it anteriorly; the styloglossus lifts the tongue and retracts it; the palatoglossus elevates the back of the tongue; and the hyoglossus depresses and flattens it. The muscles of the anterior neck facilitate swallowing and speech, stabilize the hyoid bone and position the larynx. The muscles of the neck stabilize and move the head. The sternocleidomastoid divides the neck into anterior and posterior triangles.

The muscles of the back and neck that move the vertebral column are complex, overlapping, and can be divided into five groups. The splenius group includes the splenius capitis and the splenius cervicis. The erector spinae has three subgroups. The iliocostalis group includes the iliocostalis cervicis, the iliocostalis thoracis, and the iliocostalis lumborum. The longissimus group includes the longissimus capitis, the longissimus cervicis, and the longissimus thoracis. The spinalis group includes the spinalis capitis, the spinalis cervicis, and the spinalis thoracis. The transversospinales include the semispinalis capitis, semispinalis cervicis, semispinalis thoracis, multifidus, and rotatores. The segmental muscles include the interspinales and intertransversarii. Finally, the scalenes include the anterior scalene, middle scalene, and posterior scalene.

11.4 Axial Muscles of the Abdominal Wall, and Thorax

Made of skin, fascia, and four pairs of muscle, the anterior abdominal wall protects the organs located in the abdomen and moves the vertebral column. These muscles include the rectus abdominis, which extends through the entire length of the trunk, the external oblique, the internal oblique, and the transversus abdominis. The quadratus lumborum forms the posterior abdominal wall.

The muscles of the thorax play a large role in breathing, especially the dome-shaped diaphragm. When it contracts and flattens, the volume inside the pleural cavities increases, which decreases the pressure within them. As a result, air will flow into the lungs. The external and internal intercostal muscles span the space between the ribs and help change the shape of the rib cage and the volume-pressure ratio inside the pleural cavities during inspiration and expiration.

The perineum muscles play roles in urination in both sexes, ejaculation in males, and vaginal contraction in females. The pelvic floor muscles support the pelvic organs, resist intra-abdominal pressure, and work as sphincters for the urethra, rectum, and vagina.

11.5 Muscles of the Pectoral Girdle and Upper Limbs

The clavicle and scapula make up the pectoral girdle, which provides a stable origin for the muscles that move the humerus. The muscles that position and stabilize the pectoral girdle are located on the thorax. The anterior thoracic muscles are the subclavius, pectoralis minor, and the serratus anterior. The posterior thoracic muscles are the trapezius, levator scapulae, rhomboid major, and rhomboid minor. Nine muscles cross the shoulder joint to move the humerus. The ones that originate on the axial skeleton are the pectoralis major and the latissimus dorsi. The deltoid, subscapularis, supraspinatus, infraspinatus, teres major, teres minor, and coracobrachialis originate on the scapula.

The forearm flexors include the biceps brachii, brachialis, and brachioradialis. The extensors are the

triceps brachii and anconeus. The pronators are the pronator teres and the pronator quadratus. The supinator is the only one that turns the forearm anteriorly.

The extrinsic muscles of the hands originate along the forearm and insert into the hand in order to facilitate crude movements of the wrists, hands, and fingers. The superficial anterior compartment of the forearm produces flexion. These muscles are the flexor carpi radialis, palmaris longus, flexor carpi ulnaris, and the flexor digitorum superficialis. The deep anterior compartment produces flexion as well. These are the flexor pollicis longus and the flexor digitorum profundus. The rest of the compartments produce extension. The extensor carpi radialis longus, extensor carpi radialis brevis, extensor digitorum, extensor digiti minimi, and extensor carpi ulnaris are the muscles found in the superficial posterior compartment. The deep posterior compartment includes the abductor longus, extensor pollicis brevis, extensor pollicis longus, and the extensor indicis.

Finally, the intrinsic muscles of the hands allow our fingers to make precise movements, such as typing and writing. They both originate and insert within the hand. The thenar muscles, which are located on the lateral part of the palm, are the abductor pollicis brevis, opponens pollicis, flexor pollicis brevis, and adductor pollicis. The hypothenar muscles, which are located on the medial part of the palm, are the abductor digiti minimi, flexor digiti minimi brevis, and opponens digiti minimi. The intermediate muscles, located in the middle of the palm, are the lumbricals, palmar interossei, and dorsal interossei.

11.6 Appendicular Muscles of the Pelvic Girdle and Lower Limbs

The pelvic girdle attaches the legs to the axial skeleton. The hip joint is where the pelvic girdle and the leg come together. The hip is joined to the pelvic girdle by many muscles. In the gluteal region, the psoas major and iliacus form the iliopsoas. The large and strong gluteus maximus, gluteus medius, and gluteus minimus extend and abduct the femur. Along with the gluteus maximus, the tensor fascia lata muscle forms the iliotibial tract. The lateral rotators of the femur at the hip are the piriformis, obturator internus, obturator externus, superior gemellus, inferior gemellus, and quadratus femoris. On the medial part of the thigh, the adductor longus, adductor brevis, and adductor magnus adduct the thigh and medially rotate it. The pectineus muscle adducts and flexes the femur at the hip.

The thigh muscles that move the femur, tibia, and fibula are divided into medial, anterior, and posterior compartments. The medial compartment includes the adductors, pectineus, and the gracilis. The anterior compartment comprises the quadriceps femoris, quadriceps tendon, patellar ligament, and the sartorius. The quadriceps femoris is made of four muscles: the rectus femoris, the vastus lateralis, the vastus medius, and the vastus intermedius, which together extend the knee. The posterior compartment of the thigh includes the hamstrings: the biceps femoris, semitendinosus, and the semimembranosus, which all flex the knee.

The muscles of the leg that move the foot and toes are divided into anterior, lateral, superficial- and deep-posterior compartments. The anterior compartment includes the tibialis anterior, the extensor hallucis longus, the extensor digitorum longus, and the fibularis (peroneus) tertius. The lateral compartment houses the fibularis (peroneus) longus and the fibularis (peroneus) brevis. The superficial posterior compartment has the gastrocnemius, soleus, and plantaris; and the deep posterior compartment has the popliteus, tibialis posterior, flexor digitorum longus, and flexor hallucis longus.

Review Questions

1. Which of the following is unique to the muscles of facial expression?
   a. They all originate from the scalp musculature.
   b. They insert onto the cartilage found around the face.
   c. They only insert onto the facial bones.
   d. They insert into the skin.

2. Which of the following helps an agonist work?
   a. a synergist
   b. a fixator
   c. an insertion
   d. an antagonist

3. Which of the following statements is correct about what happens during flexion?
   a. The angle between bones is increased.
   b. The angle between bones is decreased.
   c. The bone moves away from the body.
   d. The bone moves toward the center of the body.

4. Which is moved the *least* during muscle contraction?
   a. the origin
   b. the insertion
   c. the ligaments
   d. the joints

5. Which muscle has a convergent pattern of fascicles?
   a. biceps brachii
   b. gluteus maximus
   c. pectoralis major
   d. rectus femoris

6. A muscle that has a pattern of fascicles running along the long axis of the muscle has which of the following fascicle arrangements?
   a. circular
   b. pennate
   c. parallel
   d. rectus

7. Which arrangement *best* describes a bipennate muscle?
   a. The muscle fibers feed in on an angle to a long tendon from both sides.
   b. The muscle fibers feed in on an angle to a long tendon from all directions.
   c. The muscle fibers feed in on an angle to a long tendon from one side.
   d. The muscle fibers on one side of a tendon feed into it at a certain angle and muscle fibers on the other side of the tendon feed into it at the opposite angle.

8. The location of a muscle's insertion and origin can determine _____.
   a. action
   b. the force of contraction
   c. muscle name
   d. the load a muscle can carry

9. Where is the temporalis muscle located?
   a. on the forehead
   b. in the neck
   c. on the side of the head
   d. on the chin

10. Which muscle name does *not* make sense?
   a. extensor digitorum
   b. gluteus minimus
   c. biceps femoris
   d. extensor minimus longus

11. Which of the following terms would be used in the name of a muscle that moves the leg away from the body?
   a. flexor
   b. adductor
   c. extensor
   d. abductor

12. Which of the following is a prime mover in head flexion?
   a. occipitofrontalis
   b. corrugator supercilii
   c. sternocleidomastoid
   d. masseter

13. Where is the inferior oblique muscle located?
   a. in the abdomen
   b. in the eye socket
   c. in the anterior neck
   d. in the face

14. What is the action of the masseter?
   a. swallowing
   b. chewing
   c. moving the lips
   d. closing the eye

15. The names of the extrinsic tongue muscles commonly end in _____.
   a. -glottis
   b. -glossus
   c. -gluteus
   d. -hyoid

16. What is the function of the erector spinae?
   a. movement of the arms
   b. stabilization of the pelvic girdle
   c. postural support
   d. rotating of the vertebral column

17. Which of the following abdominal muscles is not a part of the anterior abdominal wall?
   a. quadratus lumborum
   b. rectus abdominis
   c. interior oblique
   d. exterior oblique

18. Which muscle pair plays a role in respiration?
   a. intertransversarii, interspinales
   b. semispinalis cervicis, semispinalis thoracis
   c. trapezius, rhomboids
   d. diaphragm, scalene

19. What is the linea alba?
   a. a small muscle that helps with compression of the abdominal organs
   b. a long tendon that runs down the middle of the rectus abdominis
   c. a long band of collagen fibers that connects the hip to the knee
   d. another name for the tendinous inscription

20. The rhomboid major and minor muscles are deep to the _____.
   a. rectus abdominis
   b. scalene muscles
   c. trapezius
   d. ligamentum nuchae

21. Which muscle extends the forearm?
   a. biceps brachii
   b. triceps brachii
   c. brachialis
   d. deltoid

22. What is the origin of the wrist flexors?
   a. the lateral epicondyle of the humerus
   b. the medial epicondyle of the humerus
   c. the carpal bones of the wrist
   d. the deltoid tuberosity of the humerus

23. Which muscles stabilize the pectoral girdle?
   a. axial and scapular
   b. axial
   c. appendicular
   d. axial and appendicular

24. The large muscle group that attaches the leg to the pelvic girdle and produces extension of the hip joint is the _____ group.
   a. gluteal
   b. obturator
   c. adductor
   d. abductor

25. Which muscle produces movement that allows you to cross your legs?
   a. the gluteus maximus
   b. the piriformis
   c. the gracilis
   d. the sartorius

26. What is the largest muscle in the lower leg?
   a. soleus
   b. gastrocnemius
   c. tibialis anterior
   d. tibialis posterior

27. The vastus intermedius muscle is deep to which of the following muscles?
   a. biceps femoris
   b. rectus femoris
   c. vastus medialis
   d. vastus lateralis

Critical Thinking Questions

28. What effect does fascicle arrangement have on a muscle's action?

29. Movements of the body occur at joints. Describe how muscles are arranged around the joints of the body.

30. Explain how a synergist assists an agonist by being a fixator.

31. Describe the different criteria that contribute to how skeletal muscles are named.

32. Explain the difference between axial and appendicular muscles.

33. Describe the muscles of the anterior neck.

34. Why are the muscles of the face different from typical skeletal muscle?

35. Describe the fascicle arrangement in the muscles of the abdominal wall. How do they relate to each other?

36. What are some similarities and differences between the diaphragm and the pelvic diaphragm?

37. The tendons of which muscles form the rotator cuff? Why is the rotator cuff important?

38. List the general muscle groups of the shoulders and upper limbs as well as their subgroups.

39. Which muscles form the hamstrings? How do they function together?

40. Which muscles form the quadriceps? How do they function together?

CHAPTER 12
The Nervous System and Nervous Tissue

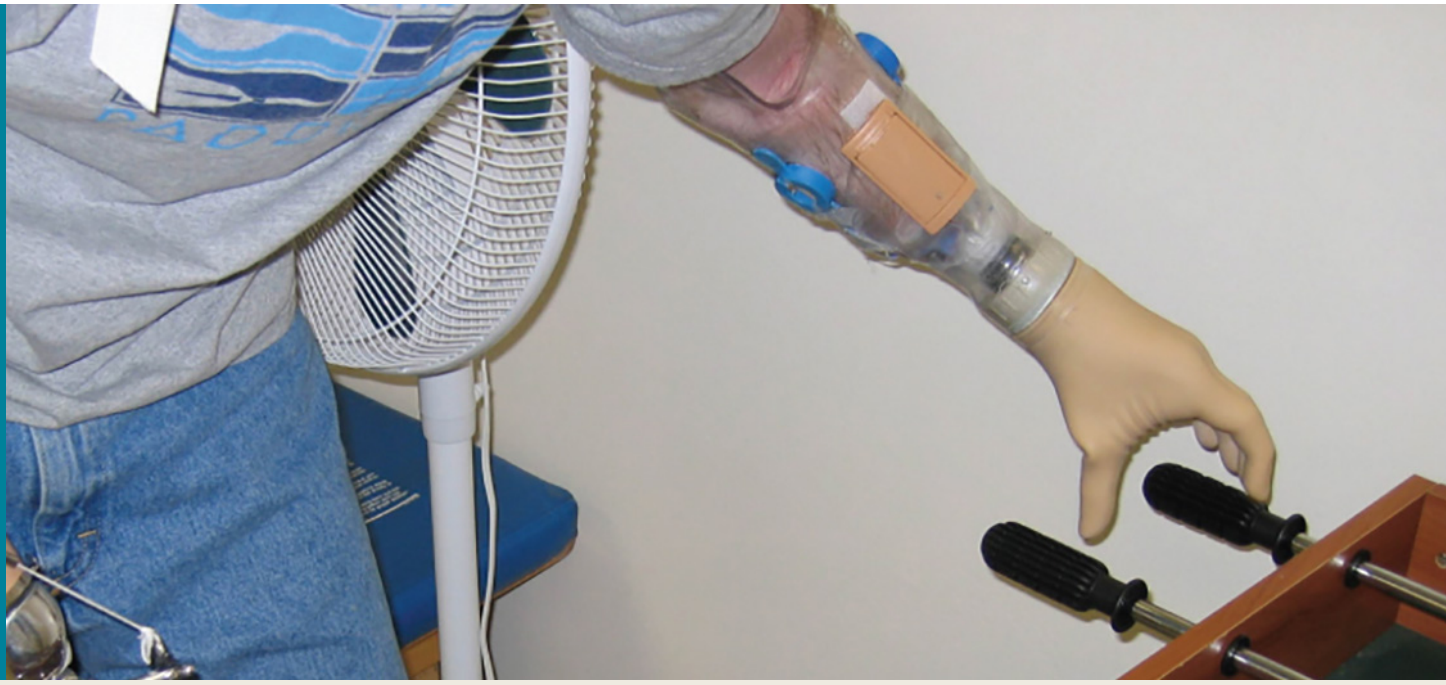


Figure 12.1 **Robotic Arms Playing Foosball** As the neural circuitry of the nervous system has become more fully understood and robotics more sophisticated, it is now possible to integrate technology with the body and restore abilities following traumatic events. At some point in the future, will this type of technology lead to the ability to augment our nervous systems? (credit: U.S. Army/Wikimedia Commons)

CHAPTER OBJECTIVES

After studying this chapter, you will be able to:

- Name the major divisions of the nervous system, both anatomical and functional
- Describe the functional and structural differences between gray matter and white matter structures
- Name the parts of the multipolar neuron in order of polarity
- List the types of glial cells and assign each to the proper division of the nervous system, along with their function(s)
- Distinguish the major functions of the nervous system: sensation, integration, and response
- Describe the components of the membrane that establish the resting membrane potential
- Describe the changes that occur to the membrane that result in the action potential
- Explain the differences between types of graded potentials
- Categorize the major neurotransmitters by chemical type and effect

INTRODUCTION The nervous system is a very complex organ system. In Peter D. Kramer's book *Listening to Prozac*, a pharmaceutical researcher is quoted as saying, "If the human brain were simple enough for us to understand, we would be too simple to understand it" (1994). That quote is from the early 1990s; in the two decades since, progress has continued at an amazing rate within the scientific disciplines of neuroscience. It is an interesting conundrum to consider that the complexity of the nervous system may be too complex for it (that is, for us) to completely unravel. But our current level of understanding is probably nowhere close to that limit.

One easy way to begin to understand the structure of the nervous system is to start with the large divisions and work through to a more in-depth understanding. In other chapters, the finer details of the nervous system will be explained, but first looking at an overview of the system will allow you to begin to understand how its parts work together. The focus of this chapter is on nervous (neural) tissue, both its structure and its function. But before you learn about that, you will see a big picture of the system—actually, a few big pictures.

12.1 Basic Structure and Function of the Nervous System

LEARNING OBJECTIVES

By the end of this section, you will be able to:

- Identify the anatomical and functional divisions of the nervous system
- Relate the functional and structural differences between gray matter and white matter structures of the nervous system to the structure of neurons
- List the basic functions of the nervous system

The picture you have in your mind of the nervous system probably includes the **brain**, the nervous tissue contained within the cranium, and the **spinal cord**, the extension of nervous tissue within the vertebral column. That suggests it is made of two organs—and you may not even think of the spinal cord as an organ—but the nervous system is a very complex structure. Within the brain, many different and separate regions are responsible for many different and separate functions. It is as if the nervous system is composed of many organs that all look similar and can only be differentiated using tools such as the microscope or electrophysiology. In comparison, it is easy to see that the stomach is different than the esophagus or the liver, so you can imagine the digestive system as a collection of specific organs.

The Central and Peripheral Nervous Systems

The nervous system can be divided into two major regions: the central and peripheral nervous systems. The **central nervous system (CNS)** is the brain and spinal cord, and the **peripheral nervous system (PNS)** is everything else (Figure 12.2). The brain is contained within the cranial cavity of the skull, and the spinal cord is contained within the vertebral cavity of the vertebral column. It is a bit of an oversimplification to say that the CNS is what is inside these two cavities and the peripheral nervous system is outside of them, but that is one way to start to think about it. In actuality, there are some elements of the peripheral nervous system that are within the cranial or vertebral cavities. The peripheral nervous system is so named because it is on the periphery—meaning beyond the brain and spinal cord. Depending on different aspects of the nervous system, the dividing line between central and peripheral is not necessarily universal.

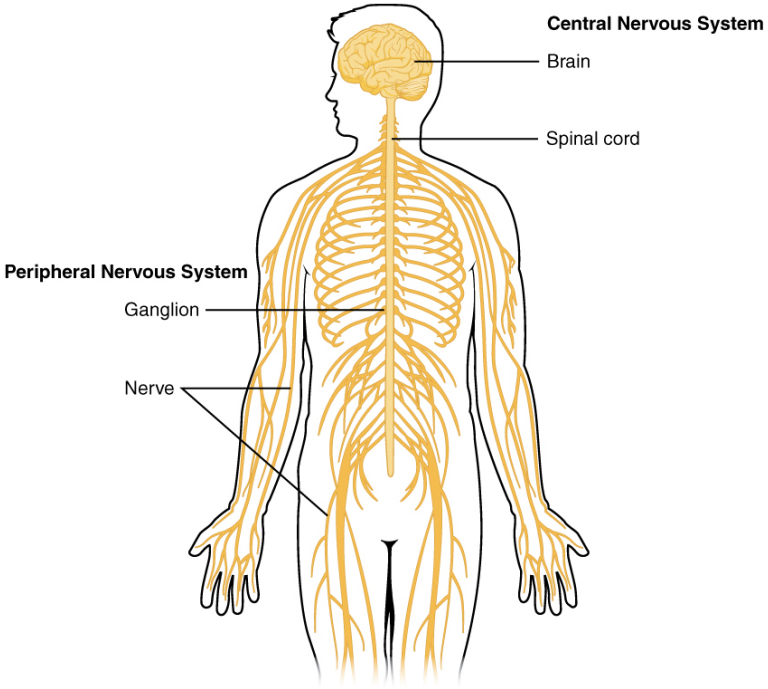


FIGURE 12.2 Central and Peripheral Nervous System The structures of the PNS are referred to as ganglia and nerves, which can be seen as distinct structures. The equivalent structures in the CNS are not obvious from this overall perspective and are best examined in prepared tissue under the microscope.

Nervous tissue, present in both the CNS and PNS, contains two basic types of cells: neurons and glial cells. A **glial cell** is one of a variety of cells that provide a framework of tissue that supports the neurons and their activities. The

neuron is the more functionally important of the two, in terms of the communicative function of the nervous system. To describe the functional divisions of the nervous system, it is important to understand the structure of a neuron. Neurons are cells and therefore have a **soma**, or cell body, but they also have extensions of the cell; each extension is generally referred to as a **process**. There is one important process that every neuron has called an **axon**, which is the fiber that connects a neuron with its target. Another type of process that branches off from the soma is the **dendrite**. Dendrites are responsible for receiving most of the input from other neurons. Looking at nervous tissue, there are regions that predominantly contain cell bodies and regions that are largely composed of just axons. These two regions within nervous system structures are often referred to as **gray matter** (the regions with many cell bodies and dendrites) or **white matter** (the regions with many axons). Figure 12.3 demonstrates the appearance of these regions in the brain and spinal cord. The colors ascribed to these regions are what would be seen in "fresh," or unstained, nervous tissue. Gray matter is not necessarily gray. It can be pinkish because of blood content, or even slightly tan, depending on how long the tissue has been preserved. But white matter is white because axons are insulated by a lipid-rich substance called **myelin**. Lipids can appear as white ("fatty") material, much like the fat on a raw piece of chicken or beef. Actually, gray matter may have that color ascribed to it because next to the white matter, it is just darker—hence, gray.

The distinction between gray matter and white matter is most often applied to central nervous tissue, which has large regions that can be seen with the unaided eye. When looking at peripheral structures, often a microscope is used and the tissue is stained with artificial colors. That is not to say that central nervous tissue cannot be stained and viewed under a microscope, but unstained tissue is most likely from the CNS—for example, a frontal section of the brain or cross section of the spinal cord.

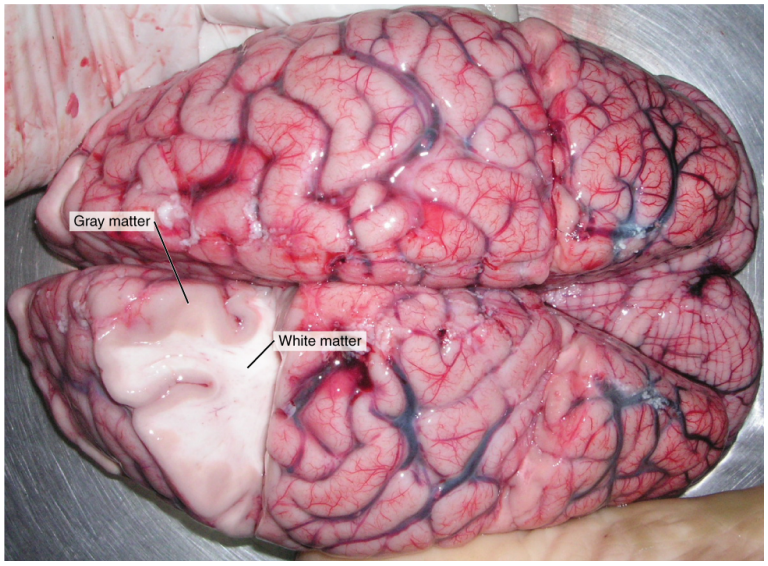


FIGURE 12.3 Gray Matter and White Matter A brain removed during an autopsy, with a partial section removed, shows white matter surrounded by gray matter. Gray matter makes up the outer cortex of the brain. (credit: modification of work by "Suseno"/Wikimedia Commons)

Regardless of the appearance of stained or unstained tissue, the cell bodies of neurons or axons can be located in discrete anatomical structures that need to be named. Those names are specific to whether the structure is central or peripheral. A localized collection of neuron cell bodies in the CNS is referred to as a **nucleus**. In the PNS, a cluster of neuron cell bodies is referred to as a **ganglion**. Figure 12.4 indicates how the term nucleus has a few different meanings within anatomy and physiology. It is the center of an atom, where protons and neutrons are found; it is the center of a cell, where the DNA is found; and it is a center of some function in the CNS. There is also a potentially confusing use of the word ganglion (plural = ganglia) that has a historical explanation. In the central nervous system, there is a group of nuclei that are connected together and were once called the basal ganglia before "ganglion" became accepted as a description for a peripheral structure. Some sources refer to this group of nuclei as the "basal nuclei" to avoid confusion.

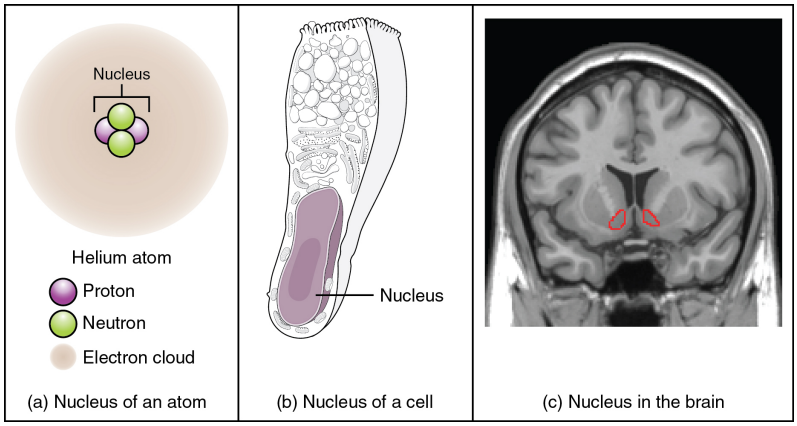


FIGURE 12.4 What Is a Nucleus? (a) The nucleus of an atom contains its protons and neutrons. (b) The nucleus of a cell is the organelle that contains DNA. (c) A nucleus in the CNS is a localized center of function with the cell bodies of several neurons, shown here circled in red. (credit c: "Was a bee"/Wikimedia Commons)

Terminology applied to bundles of axons also differs depending on location. A bundle of axons, or fibers, found in the CNS is called a **tract** whereas the same thing in the PNS would be called a **nerve**. There is an important point to make about these terms, which is that they can both be used to refer to the same bundle of axons. When those axons are in the PNS, the term is nerve, but if they are CNS, the term is tract. The most obvious example of this is the axons that project from the retina into the brain. Those axons are called the optic nerve as they leave the eye, but when they are inside the cranium, they are referred to as the optic tract. There is a specific place where the name changes, which is the optic chiasm, but they are still the same axons (Figure 12.5). A similar situation outside of science can be described for some roads. Imagine a road called "Broad Street" in a town called "Anyville." The road leaves Anyville and goes to the next town over, called "Hometown." When the road crosses the line between the two towns and is in Hometown, its name changes to "Main Street." That is the idea behind the naming of the retinal axons. In the PNS, they are called the optic nerve, and in the CNS, they are the optic tract. Table 12.1 helps to clarify which of these terms apply to the central or peripheral nervous systems.

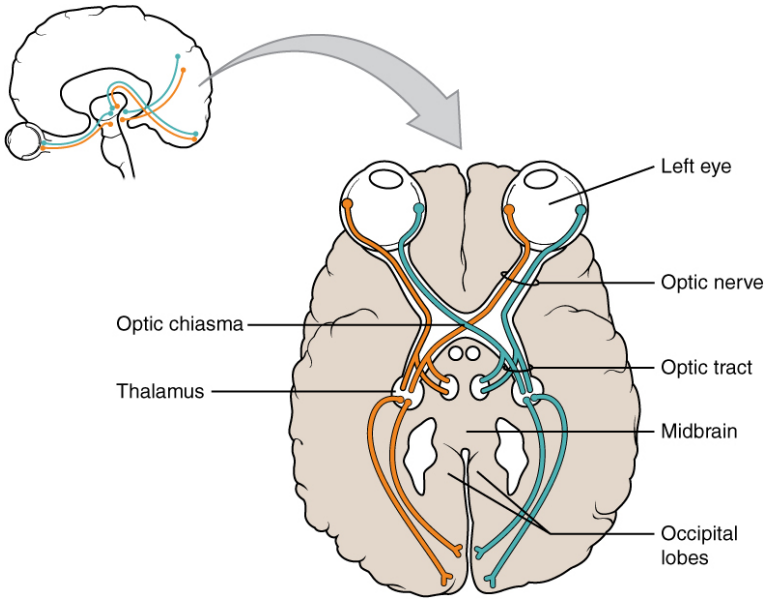


FIGURE 12.5 Optic Nerve Versus Optic Tract This drawing of the connections of the eye to the brain shows the optic nerve extending from the eye to the chiasm, where the structure continues as the optic tract. The same axons extend from the eye to the brain through these two bundles of fibers, but the chiasm represents the border between peripheral and central.

INTERACTIVE LINK

In 2003, the Nobel Prize in Physiology or Medicine was awarded to Paul C. Lauterbur and Sir Peter Mansfield for discoveries related to magnetic resonance imaging (MRI). This is a tool to see the structures of the body (not just the nervous system) that depends on magnetic fields associated with certain atomic nuclei. The utility of this technique

in the nervous system is that fat tissue and water appear as different shades between black and white. Because white matter is fatty (from myelin) and gray matter is not, they can be easily distinguished in MRI images. Try this PhET simulation (http://openstax.org/l/nobel_2) that demonstrates the use of this technology and compares it with other types of imaging technologies. Also, the results from an MRI session are compared with images obtained from X-ray or computed tomography. How do the imaging techniques shown in this game indicate the separation of white and gray matter compared with the freshly dissected tissue shown earlier?

Structures of the CNS and PNS

	CNS	PNS
Group of Neuron Cell Bodies (i.e., gray matter)	Nucleus	Ganglion
Bundle of Axons (i.e., white matter)	Tract	Nerve

TABLE 12.1

Functional Divisions of the Nervous System

The nervous system can also be divided on the basis of its functions, but anatomical divisions and functional divisions are different. The CNS and the PNS both contribute to the same functions, but those functions can be attributed to different regions of the brain (such as the cerebral cortex or the hypothalamus) or to different ganglia in the periphery. The problem with trying to fit functional differences into anatomical divisions is that sometimes the same structure can be part of several functions. For example, the optic nerve carries signals from the retina that are either used for the conscious perception of visual stimuli, which takes place in the cerebral cortex, or for the reflexive responses of smooth muscle tissue that are processed through the hypothalamus.

There are two ways to consider how the nervous system is divided functionally. First, the basic functions of the nervous system are sensation, integration, and response. Secondly, control of the body can be somatic or autonomic—divisions that are largely defined by the structures that are involved in the response. There is also a region of the peripheral nervous system that is called the enteric nervous system that is responsible for a specific set of the functions within the realm of autonomic control related to gastrointestinal functions.

Basic Functions

The nervous system is involved in receiving information about the environment around us (sensation) and generating responses to that information (motor responses). The nervous system can be divided into regions that are responsible for **sensation** (sensory functions) and for the **response** (motor functions). But there is a third function that needs to be included. Sensory input needs to be integrated with other sensations, as well as with memories, emotional state, or learning (cognition). Some regions of the nervous system are termed **integration** or association areas. The process of integration combines sensory perceptions and higher cognitive functions such as memories, learning, and emotion to produce a response.

Sensation. The first major function of the nervous system is sensation—receiving information about the environment to gain input about what is happening outside the body (or, sometimes, within the body). The sensory functions of the nervous system register the presence of a change from homeostasis or a particular event in the environment, known as a **stimulus**. The senses we think of most are the "big five": taste, smell, touch, sight, and hearing. The stimuli for taste and smell are both chemical substances (molecules, compounds, ions, etc.), touch is physical or mechanical stimuli that interact with the skin, sight is light stimuli, and hearing is the perception of sound, which is a physical stimulus similar to some aspects of touch. There are actually more senses than just those, but that list represents the major senses. Those five are all senses that receive stimuli from the outside world, and of which there is conscious perception. Additional sensory stimuli might be from the internal environment (inside the body), such as the stretch of an organ wall or the concentration of certain ions in the blood.

Response. The nervous system produces a response on the basis of the stimuli perceived by sensory structures. An obvious response would be the movement of muscles, such as withdrawing a hand from a hot stove, but there are

broader uses of the term. The nervous system can cause the contraction of all three types of muscle tissue. For example, skeletal muscle contracts to move the skeleton, cardiac muscle is influenced as heart rate increases during exercise, and smooth muscle contracts as the digestive system moves food along the digestive tract. Responses also include the neural control of glands in the body as well, such as the production and secretion of sweat by the eccrine and merocrine sweat glands found in the skin to lower body temperature.

Responses can be divided into those that are voluntary or conscious (contraction of skeletal muscle) and those that are involuntary (contraction of smooth muscles, regulation of cardiac muscle, activation of glands). Voluntary responses are governed by the somatic nervous system and involuntary responses are governed by the autonomic nervous system, which are discussed in the next section.

Integration. Stimuli that are received by sensory structures are communicated to the nervous system where that information is processed. This is called integration. Stimuli are compared with, or integrated with, other stimuli, memories of previous stimuli, or the state of a person at a particular time. This leads to the specific response that will be generated. Seeing a baseball pitched to a batter will not automatically cause the batter to swing. The trajectory of the ball and its speed will need to be considered. Maybe the count is three balls and one strike, and the batter wants to let this pitch go by in the hope of getting a walk to first base. Or maybe the batter's team is so far ahead, it would be fun to just swing away.

Controlling the Body

The nervous system can be divided into two parts mostly on the basis of a functional difference in responses. The **somatic nervous system (SNS)** is responsible for conscious perception and voluntary motor responses. Voluntary motor response means the contraction of skeletal muscle, but those contractions are not always voluntary in the sense that you have to want to perform them. Some somatic motor responses are reflexes, and often happen without a conscious decision to perform them. If your friend jumps out from behind a corner and yells "Boo!" you will be startled and you might scream or leap back. You didn't decide to do that, and you may not have wanted to give your friend a reason to laugh at your expense, but it is a reflex involving skeletal muscle contractions. Other motor responses become automatic (in other words, unconscious) as a person learns motor skills (referred to as "habit learning" or "procedural memory").

The **autonomic nervous system (ANS)** is responsible for involuntary control of the body, usually for the sake of homeostasis (regulation of the internal environment). Sensory input for autonomic functions can be from sensory structures tuned to external or internal environmental stimuli. The motor output extends to smooth and cardiac muscle as well as glandular tissue. The role of the autonomic system is to regulate the organ systems of the body, which usually means to control homeostasis. Sweat glands, for example, are controlled by the autonomic system. When you are hot, sweating helps cool your body down. That is a homeostatic mechanism. But when you are nervous, you might start sweating also. That is not homeostatic, it is the physiological response to an emotional state.

There is another division of the nervous system that describes functional responses. The **enteric nervous system (ENS)** is responsible for controlling the smooth muscle and glandular tissue in your digestive system. It is a large part of the PNS, and is not dependent on the CNS. It is sometimes valid, however, to consider the enteric system to be a part of the autonomic system because the neural structures that make up the enteric system are a component of the autonomic output that regulates digestion. There are some differences between the two, but for our purposes here there will be a good bit of overlap. See Figure 12.6 for examples of where these divisions of the nervous system can be found.

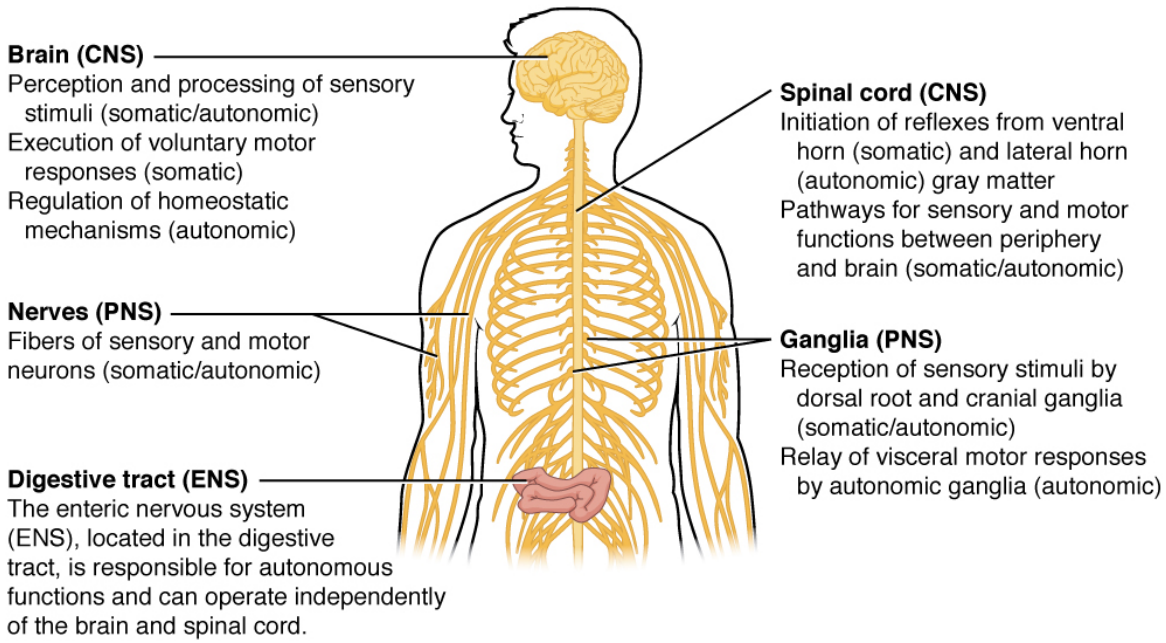


FIGURE 12.6 Somatic, Autonomic, and Enteric Structures of the Nervous System Somatic structures include the spinal nerves, both motor and sensory fibers, as well as the sensory ganglia (posterior root ganglia and cranial nerve ganglia). Autonomic structures are found in the nerves also, but include the sympathetic and parasympathetic ganglia. The enteric nervous system includes the nervous tissue within the organs of the digestive tract.

INTERACTIVE LINK

Visit this site (http://openstax.org/l/troublewstairs) to read about a woman that notices that her daughter is having trouble walking up the stairs. This leads to the discovery of a hereditary condition that affects the brain and spinal cord. The electromyography and MRI tests indicated deficiencies in the spinal cord and cerebellum, both of which are responsible for controlling coordinated movements. To what functional division of the nervous system would these structures belong?

Everyday Connection

How Much of Your Brain Do You Use?

Have you ever heard the claim that humans only use 10 percent of their brains? Maybe you have seen an advertisement on a website saying that there is a secret to unlocking the full potential of your mind—as if there were 90 percent of your brain sitting idle, just waiting for you to use it. If you see an ad like that, don't click. It isn't true.

An easy way to see how much of the brain a person uses is to take measurements of brain activity while performing a task. An example of this kind of measurement is functional magnetic resonance imaging (fMRI), which generates a map of the most active areas and can be generated and presented in three dimensions (Figure 12.7). This procedure is different from the standard MRI technique because it is measuring changes in the tissue in time with an experimental condition or event.

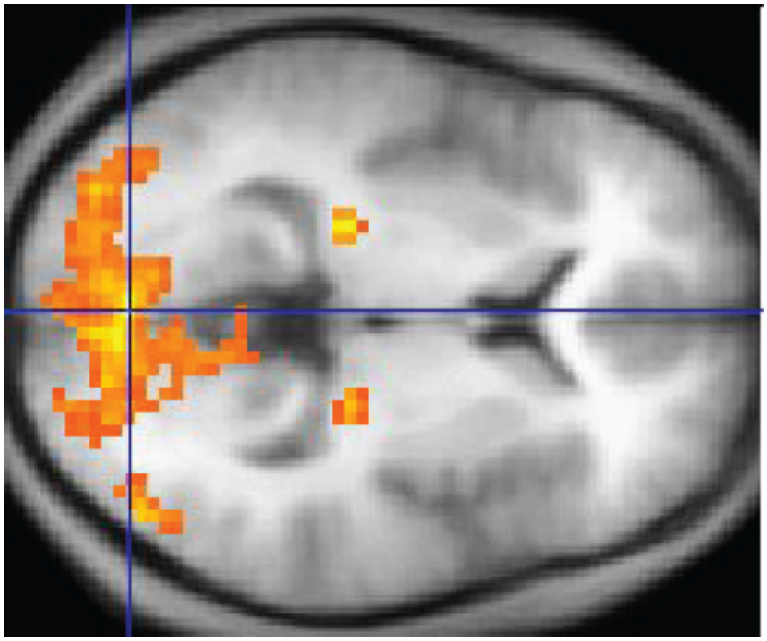


FIGURE 12.7 fMRI This fMRI shows activation of the visual cortex in response to visual stimuli. (credit: "Superborsuk"/Wikimedia Commons)

The underlying assumption is that active nervous tissue will have greater blood flow. By having the subject perform a visual task, activity all over the brain can be measured. Consider this possible experiment: the subject is told to look at a screen with a black dot in the middle (a fixation point). A photograph of a face is projected on the screen away from the center. The subject has to look at the photograph and decipher what it is. The subject has been instructed to push a button if the photograph is of someone they recognize. The photograph might be of a celebrity, so the subject would press the button, or it might be of a random person unknown to the subject, so the subject would not press the button.

In this task, visual sensory areas would be active, integrating areas would be active, motor areas responsible for moving the eyes would be active, and motor areas for pressing the button with a finger would be active. Those areas are distributed all around the brain and the fMRI images would show activity in more than just 10 percent of the brain (some evidence suggests that about 80 percent of the brain is using energy—based on blood flow to the tissue—during well-defined tasks similar to the one suggested above). This task does not even include all of the functions the brain performs. There is no language response, the body is mostly lying still in the MRI machine, and it does not consider the autonomic functions that would be ongoing in the background.

12.2 Nervous Tissue

LEARNING OBJECTIVES

By the end of this section, you will be able to:

- Describe the basic structure of a neuron
- Identify the different types of neurons on the basis of polarity
- List the glial cells of the CNS and describe their function
- List the glial cells of the PNS and describe their function

Nervous tissue is composed of two types of cells, neurons and glial cells. Neurons are the primary type of cell that most anyone associates with the nervous system. They are responsible for the computation and communication that the nervous system provides. They are electrically active and release chemical signals to target cells. Glial cells, or glia, are known to play a supporting role for nervous tissue. Ongoing research pursues an expanded role that glial cells might play in signaling, but neurons are still considered the basis of this function. Neurons are important, but without glial support they would not be able to perform their function.

Neurons

Neurons are the cells considered to be the basis of nervous tissue. They are responsible for the electrical signals that communicate information about sensations, and that produce movements in response to those stimuli, along with inducing thought processes within the brain. An important part of the function of neurons is in their structure, or shape. The three-dimensional shape of these cells makes the immense numbers of connections within the nervous system possible.

Parts of a Neuron

As you learned in the first section, the main part of a neuron is the cell body, which is also known as the soma (soma = "body"). The cell body contains the nucleus and most of the major organelles. But what makes neurons special is that they have many extensions of their cell membranes, which are generally referred to as processes. Neurons are usually described as having one, and only one, axon—a fiber that emerges from the cell body and projects to target cells. That single axon can branch repeatedly to communicate with many target cells. It is the axon that propagates the nerve impulse, which is communicated to one or more cells. The other processes of the neuron are dendrites, which receive information from other neurons at specialized areas of contact called **synapses**. The dendrites are usually highly branched processes, providing locations for other neurons to communicate with the cell body. Information flows through a neuron from the dendrites, across the cell body, and down the axon. This gives the neuron a polarity—meaning that information flows in this one direction. Figure 12.8 shows the relationship of these parts to one another.

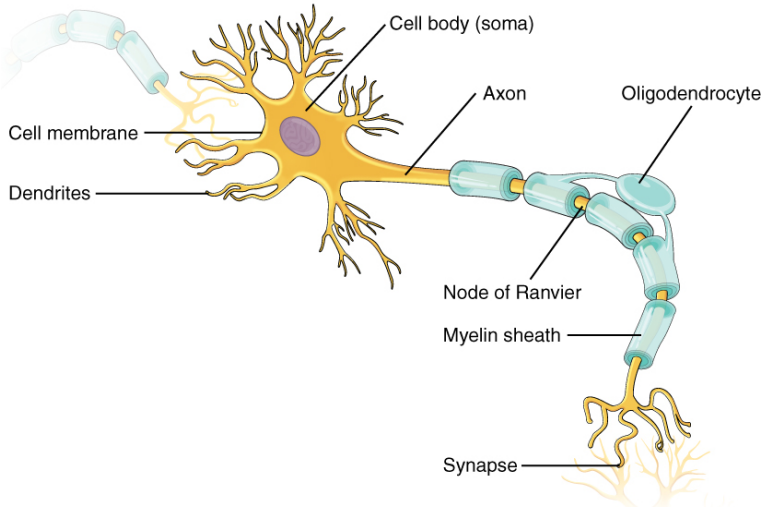


FIGURE 12.8 Parts of a Neuron The major parts of the neuron are labeled on a multipolar neuron from the CNS.

Where the axon emerges from the cell body, there is a special region referred to as the **axon hillock**. This is a tapering of the cell body toward the axon fiber. Within the axon hillock, the cytoplasm changes to a solution of limited components called **axoplasm**. Because the axon hillock represents the beginning of the axon, it is also referred to as the **initial segment**.

Many axons are wrapped by an insulating substance called myelin, which is actually made from glial cells. Myelin acts as insulation much like the plastic or rubber that is used to insulate electrical wires. A key difference between myelin and the insulation on a wire is that there are gaps in the myelin covering of an axon. Each gap is called a **node of Ranvier** and is important to the way that electrical signals travel down the axon. The length of the axon between each gap, which is wrapped in myelin, is referred to as an **axon segment**. At the end of the axon is the **axon terminal**, where there are usually several branches extending toward the target cell, each of which ends in an enlargement called a **synaptic end bulb**. These bulbs are what make the connection with the target cell at the synapse.

Types of Neurons

There are many neurons in the nervous system—a number in the trillions. And there are many different types of neurons. They can be classified by many different criteria. The first way to classify them is by the number of processes attached to the cell body. Using the standard model of neurons, one of these processes is the axon, and

the rest are dendrites. Because information flows through the neuron from dendrites or cell bodies toward the axon, these names are based on the neuron's polarity (Figure 12.9).

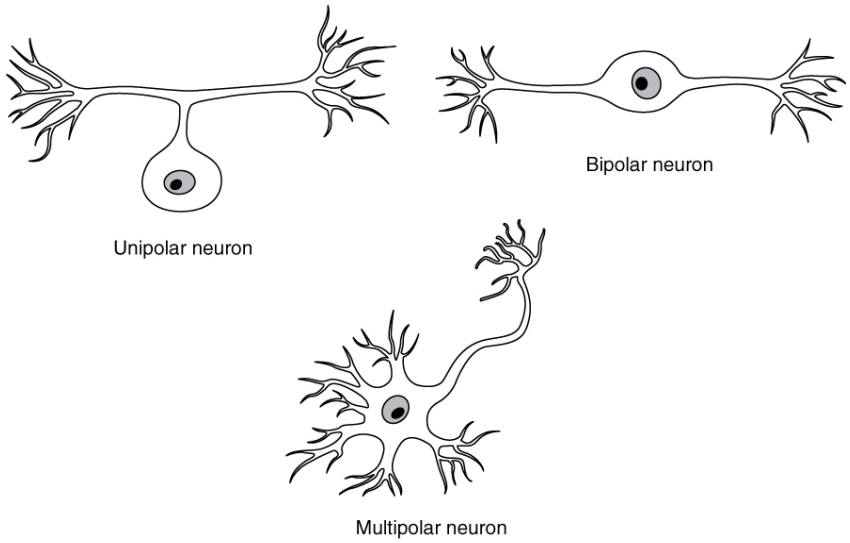


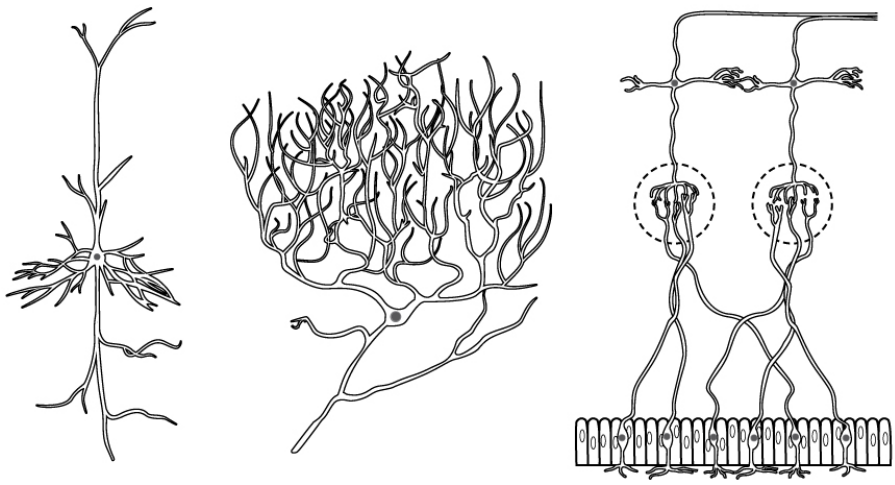
FIGURE 12.9 **Neuron Classification by Shape** Unipolar cells have one process that includes both the axon and dendrite. Bipolar cells have two processes, the axon and a dendrite. Multipolar cells have more than two processes, the axon and two or more dendrites.

Unipolar cells have only one process emerging from the cell. True unipolar cells are only found in invertebrate animals, so the unipolar cells in humans are more appropriately called "pseudo-unipolar" cells. Invertebrate unipolar cells do not have dendrites. Human unipolar cells have an axon that emerges from the cell body, but it splits so that the axon can extend along a very long distance. At one end of the axon are dendrites, and at the other end, the axon forms synaptic connections with a target. Unipolar cells are exclusively sensory neurons and have two unique characteristics. First, their dendrites are receiving sensory information, sometimes directly from the stimulus itself. Secondly, the cell bodies of unipolar neurons are always found in ganglia. Sensory reception is a peripheral function (those dendrites are in the periphery, perhaps in the skin) so the cell body is in the periphery, though closer to the CNS in a ganglion. The axon projects from the dendrite endings, past the cell body in a ganglion, and into the central nervous system.

Bipolar cells have two processes, which extend from each end of the cell body, opposite to each other. One is the axon and one the dendrite. Bipolar cells are not very common. They are found mainly in the olfactory epithelium (where smell stimuli are sensed), and as part of the retina.

Multipolar neurons are all of the neurons that are not unipolar or bipolar. They have one axon and two or more dendrites (usually many more). With the exception of the unipolar sensory ganglion cells, and the two specific bipolar cells mentioned above, all other neurons are multipolar. Some cutting edge research suggests that certain neurons in the CNS do not conform to the standard model of "one, and only one" axon. Some sources describe a fourth type of neuron, called an anaxonic neuron. The name suggests that it has no axon (an- = "without"), but this is not accurate. Anaxonic neurons are very small, and if you look through a microscope at the standard resolution used in histology (approximately 400X to 1000X total magnification), you will not be able to distinguish any process specifically as an axon or a dendrite. Any of those processes can function as an axon depending on the conditions at any given time. Nevertheless, even if they cannot be easily seen, and one specific process is definitively the axon, these neurons have multiple processes and are therefore multipolar.

Neurons can also be classified on the basis of where they are found, who found them, what they do, or even what chemicals they use to communicate with each other. Some neurons referred to in this section on the nervous system are named on the basis of those sorts of classifications (Figure 12.10). For example, a multipolar neuron that has a very important role to play in a part of the brain called the cerebellum is known as a Purkinje (commonly pronounced per-KIN-gee) cell. It is named after the anatomist who discovered it (Jan Evangelista Purkinje, 1787–1869).



(a) Pyramidal cell of the cerebral cortex

(b) Purkinje cell of the cerebellar cortex

(c) Olfactory cells in the olfactory epithelium and olfactory bulbs

FIGURE 12.10 **Other Neuron Classifications** Three examples of neurons that are classified on the basis of other criteria. (a) The pyramidal cell is a multipolar cell with a cell body that is shaped something like a pyramid. (b) The Purkinje cell in the cerebellum was named after the scientist who originally described it. (c) Olfactory neurons are named for the functional group with which they belong.

Glial Cells

Glial cells, or neuroglia or simply glia, are the other type of cell found in nervous tissue. They are considered to be supporting cells, and many functions are directed at helping neurons complete their function for communication. The name glia comes from the Greek word that means “glue,” and was coined by the German pathologist Rudolph Virchow, who wrote in 1856: “This connective substance, which is in the brain, the spinal cord, and the special sense nerves, is a kind of glue (neuroglia) in which the nervous elements are planted.” Today, research into nervous tissue has shown that there are many deeper roles that these cells play. And research may find much more about them in the future.

There are six types of glial cells. Four of them are found in the CNS and two are found in the PNS. Table 12.2 outlines some common characteristics and functions.

Glial Cell Types by Location and Basic Function

CNS glia	PNS glia	Basic function
Astrocyte	Satellite cell	Support
Oligodendrocyte	Schwann cell	Insulation, myelination
Microglia	-	Immune surveillance and phagocytosis
Ependymal cell	-	Creating CSF

TABLE 12.2

Glial Cells of the CNS

One cell providing support to neurons of the CNS is the **astrocyte**, so named because it appears to be star-shaped under the microscope (astro- = “star”). Astrocytes have many processes extending from their main cell body (not axons or dendrites like neurons, just cell extensions). Those processes extend to interact with neurons, blood vessels, or the connective tissue covering the CNS that is called the pia mater (Figure 12.11). Generally, they are supporting cells for the neurons in the central nervous system. Some ways in which they support neurons in the central nervous system are by maintaining the concentration of chemicals in the extracellular space, removing

excess signaling molecules, reacting to tissue damage, and contributing to the **blood-brain barrier (BBB)**. The blood-brain barrier is a physiological barrier that keeps many substances that circulate in the rest of the body from getting into the central nervous system, restricting what can cross from circulating blood into the CNS. Nutrient molecules, such as glucose or amino acids, can pass through the BBB, but other molecules cannot. This actually causes problems with drug delivery to the CNS. Pharmaceutical companies are challenged to design drugs that can cross the BBB as well as have an effect on the nervous system.

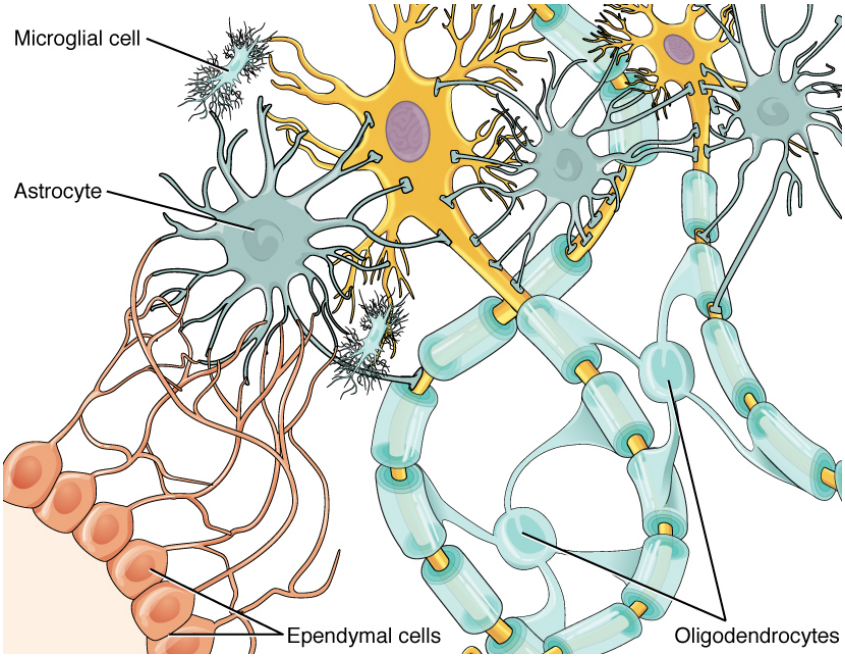


FIGURE 12.11 Glial Cells of the CNS The CNS has astrocytes, oligodendrocytes, microglia, and ependymal cells that support the neurons of the CNS in several ways.

Like a few other parts of the body, the brain has a privileged blood supply. Very little can pass through by diffusion. Most substances that cross the wall of a blood vessel into the CNS must do so through an active transport process. Because of this, only specific types of molecules can enter the CNS. Glucose—the primary energy source—is allowed, as are amino acids. Water and some other small particles, like gases and ions, can enter. But most everything else cannot, including white blood cells, which are one of the body's main lines of defense. While this barrier protects the CNS from exposure to toxic or pathogenic substances, it also keeps out the cells that could protect the brain and spinal cord from disease and damage. The BBB also makes it harder for pharmaceuticals to be developed that can affect the nervous system. Aside from finding efficacious substances, the means of delivery is also crucial.

Also found in CNS tissue is the **oligodendrocyte**, sometimes called just "oligo," which is the glial cell type that insulates axons in the CNS. The name means "cell of a few branches" (oligo- = "few"; dendro- = "branches"; -cyte = "cell"). There are a few processes that extend from the cell body. Each one reaches out and surrounds an axon to insulate it in myelin. One oligodendrocyte will provide the myelin for multiple axon segments, either for the same axon or for separate axons. The function of myelin will be discussed below.

Microglia are, as the name implies, smaller than most of the other glial cells. Ongoing research into these cells, although not entirely conclusive, suggests that they may originate as white blood cells, called macrophages, that become part of the CNS during early development. While their origin is not conclusively determined, their function is related to what macrophages do in the rest of the body. When macrophages encounter diseased or damaged cells in the rest of the body, they ingest and digest those cells or the pathogens that cause disease. Microglia are the cells in the CNS that can do this in normal, healthy tissue, and they are therefore also referred to as CNS-resident macrophages.

The **ependymal cell** is a glial cell that filters blood to make **cerebrospinal fluid (CSF)**, the fluid that circulates through the CNS. Because of the privileged blood supply inherent in the BBB, the extracellular space in nervous tissue does not easily exchange components with the blood. Ependymal cells line each **ventricle**, one of four central

cavities that are remnants of the hollow center of the neural tube formed during the embryonic development of the brain. The **choroid plexus** is a specialized structure in the ventricles where ependymal cells come in contact with blood vessels and filter and absorb components of the blood to produce cerebrospinal fluid. Because of this, ependymal cells can be considered a component of the BBB, or a place where the BBB breaks down. These glial cells appear similar to epithelial cells, making a single layer of cells with little intracellular space and tight connections between adjacent cells. They also have cilia on their apical surface to help move the CSF through the ventricular space. The relationship of these glial cells to the structure of the CNS is seen in Figure 12.11.

Glial Cells of the PNS

One of the two types of glial cells found in the PNS is the **satellite cell**. Satellite cells are found in sensory and autonomic ganglia, where they surround the cell bodies of neurons. This accounts for the name, based on their appearance under the microscope. They provide support, performing similar functions in the periphery as astrocytes do in the CNS—except, of course, for establishing the BBB.

The second type of glial cell is the **Schwann cell**, which insulate axons with myelin in the periphery. Schwann cells are different than oligodendrocytes, in that a Schwann cell wraps around a portion of only one axon segment and no others. Oligodendrocytes have processes that reach out to multiple axon segments, whereas the entire Schwann cell surrounds just one axon segment. The nucleus and cytoplasm of the Schwann cell are on the edge of the myelin sheath. The relationship of these two types of glial cells to ganglia and nerves in the PNS is seen in Figure 12.12.

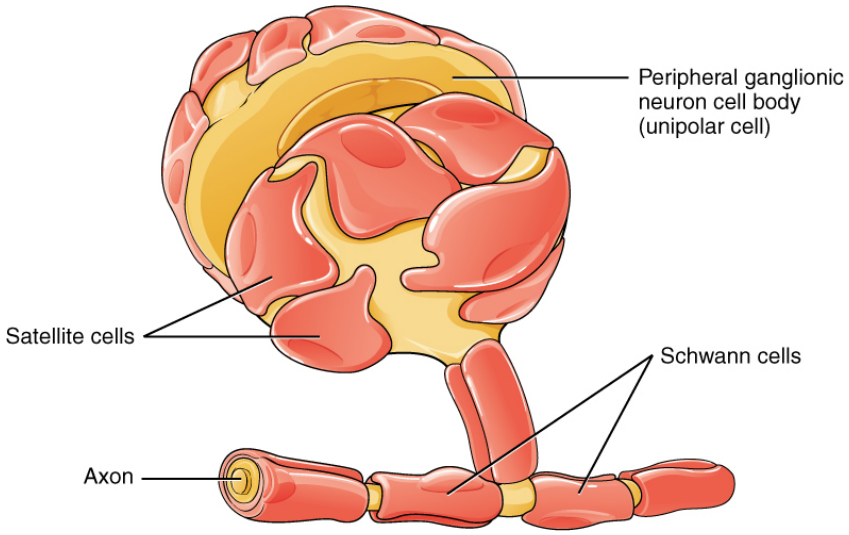


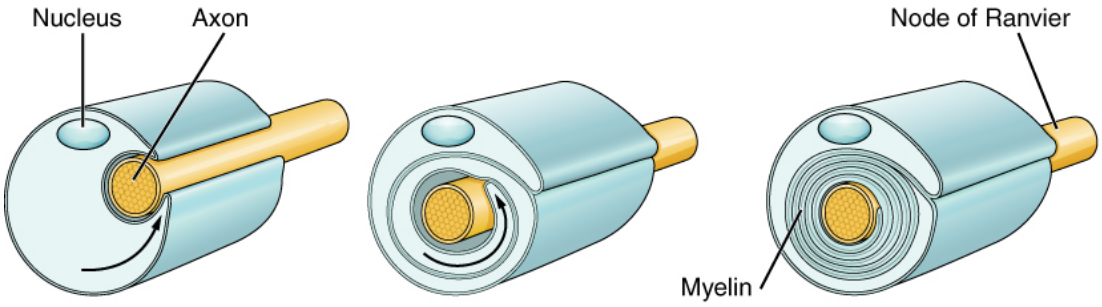
FIGURE 12.12 Glial Cells of the PNS The PNS has satellite cells and Schwann cells.

Myelin

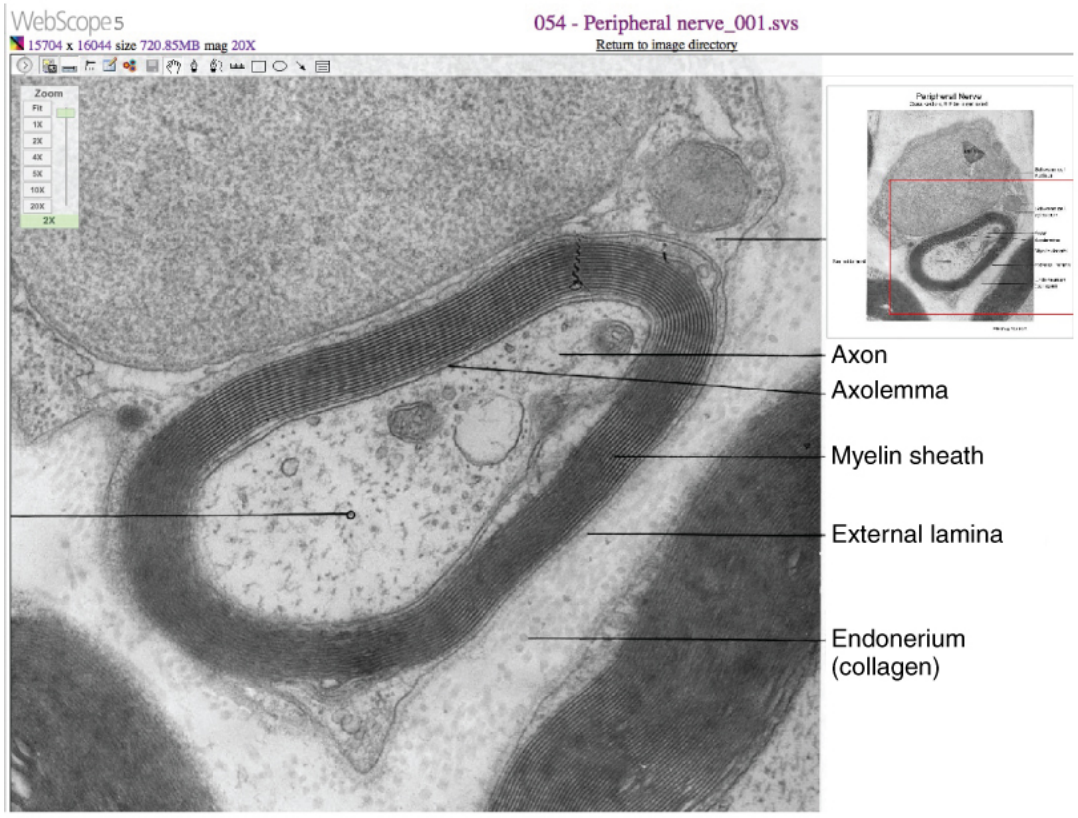
The insulation for axons in the nervous system is provided by glial cells, oligodendrocytes in the CNS, and Schwann cells in the PNS. Whereas the manner in which either cell is associated with the axon segment, or segments, that it insulates is different, the means of myelinating an axon segment is mostly the same in the two situations. Myelin is a lipid-rich sheath that surrounds the axon and by doing so creates a **myelin sheath** that facilitates the transmission of electrical signals along the axon. The lipids are essentially the phospholipids of the glial cell membrane. Myelin, however, is more than just the membrane of the glial cell. It also includes important proteins that are integral to that membrane. Some of the proteins help to hold the layers of the glial cell membrane closely together.

The appearance of the myelin sheath can be thought of as similar to the pastry wrapped around a hot dog for “pigs in a blanket” or a similar food. The glial cell is wrapped around the axon several times with little to no cytoplasm between the glial cell layers. For oligodendrocytes, the rest of the cell is separate from the myelin sheath as a cell process extends back toward the cell body. A few other processes provide the same insulation for other axon segments in the area. For Schwann cells, the outermost layer of the cell membrane contains cytoplasm and the nucleus of the cell as a bulge on one side of the myelin sheath. During development, the glial cell is loosely or incompletely wrapped around the axon (Figure 12.13**a**). The edges of this loose enclosure extend toward each other, and one end tucks under the other. The inner edge wraps around the axon, creating several layers, and the other edge closes around the outside so that the axon is completely enclosed.

Myelin sheaths can extend for one or two millimeters, depending on the diameter of the axon. Axon diameters can be as small as 1 to 20 micrometers. Because a micrometer is 1/1000 of a millimeter, this means that the length of a myelin sheath can be 100–1000 times the diameter of the axon. Figure 12.8, Figure 12.11, and Figure 12.12 show the myelin sheath surrounding an axon segment, but are not to scale. If the myelin sheath were drawn to scale, the neuron would have to be immense—possibly covering an entire wall of the room in which you are sitting.



(a)



(b)

FIGURE 12.13 **The Process of Myelination** Myelinating glia wrap several layers of cell membrane around the cell membrane of an axon segment. A single Schwann cell insulates a segment of a peripheral nerve, whereas in the CNS, an oligodendrocyte may provide insulation for a few separate axon segments. EM × 1,460,000. (Micrograph provided by the Regents of University of Michigan Medical School © 2012)

Disorders of the...

Nervous Tissue

Several diseases can result from the demyelination of axons. The causes of these diseases are not the same; some have genetic causes, some are caused by pathogens, and others are the result of autoimmune disorders. Though the causes are varied, the results are largely similar. The myelin insulation of axons is compromised,

making electrical signaling slower.

Multiple sclerosis (MS) is one such disease. It is an example of an autoimmune disease. The antibodies produced by lymphocytes (a type of white blood cell) mark myelin as something that should not be in the body. This causes inflammation and the destruction of the myelin in the central nervous system. As the insulation around the axons is destroyed by the disease, scarring becomes obvious. This is where the name of the disease comes from; sclerosis means hardening of tissue, which is what a scar is. Multiple scars are found in the white matter of the brain and spinal cord. The symptoms of MS include both somatic and autonomic deficits. Control of the musculature is compromised, as is control of organs such as the bladder.

Guillain-Barré (pronounced gee-YAN bah-RAY) syndrome is an example of a demyelinating disease of the peripheral nervous system. It is also the result of an autoimmune reaction, but the inflammation is in peripheral nerves. Sensory symptoms or motor deficits are common, and autonomic failures can lead to changes in the heart rhythm or a drop in blood pressure, especially when standing, which causes dizziness.

12.3 The Function of Nervous Tissue

LEARNING OBJECTIVES

By the end of this section, you will be able to:

- Distinguish the major functions of the nervous system: sensation, integration, and response
- List the sequence of events in a simple sensory receptor–motor response pathway

Having looked at the components of nervous tissue, and the basic anatomy of the nervous system, next comes an understanding of how nervous tissue is capable of communicating within the nervous system. Before getting to the nuts and bolts of how this works, an illustration of how the components come together will be helpful. An example is summarized in Figure 12.14.

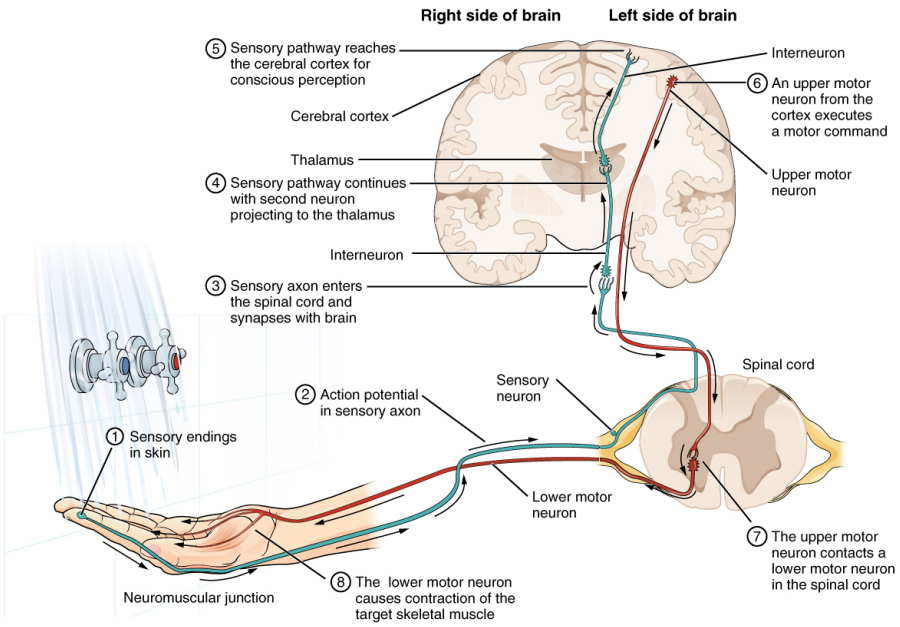


FIGURE 12.14 Testing the Water (1) The sensory neuron has endings in the skin that sense a stimulus such as water temperature. The strength of the signal that starts here is dependent on the strength of the stimulus. (2) The graded potential from the sensory endings, if strong enough, will initiate an action potential at the initial segment of the axon (which is immediately adjacent to the sensory endings in the skin). (3) The axon of the peripheral sensory neuron enters the spinal cord and contacts another neuron in the gray matter. The contact is a synapse where another graded potential is caused by the release of a chemical signal from the axon terminals. (4) An action potential is initiated at the initial segment of this neuron and travels up the sensory pathway to a region of the brain called the thalamus. Another synapse passes the information along to the next neuron. (5) The sensory pathway ends when the signal reaches the cerebral cortex. (6) After integration with neurons in other parts of the cerebral cortex, a motor command is sent from the precentral gyrus of the frontal cortex. (7) The upper motor neuron sends an action potential down to the spinal cord. The target of the upper motor neuron is the dendrites of the lower motor neuron in the gray matter of the spinal cord. (8) The axon of the lower motor neuron emerges from the spinal cord in a nerve and connects to a muscle through a neuromuscular junction to cause contraction of the target muscle.

Imagine you are about to take a shower in the morning before going to school. You have turned on the faucet to start the water as you prepare to get in the shower. After a few minutes, you expect the water to be a temperature that will be comfortable to enter. So you put your hand out into the spray of water. What happens next depends on how your nervous system interacts with the stimulus of the water temperature and what you do in response to that stimulus.

Found in the skin of your fingers or toes is a type of sensory receptor that is sensitive to temperature, called a **thermoreceptor**. When you place your hand under the shower (Figure 12.15), the cell membrane of the thermoreceptors changes its electrical state (voltage). The amount of change is dependent on the strength of the stimulus (how hot the water is). This is called a **graded potential**. If the stimulus is strong, the voltage of the cell membrane will change enough to generate an electrical signal that will travel down the axon. You have learned about this type of signaling before, with respect to the interaction of nerves and muscles at the neuromuscular junction. The voltage at which such a signal is generated is called the **threshold**, and the resulting electrical signal is called an **action potential**. In this example, the action potential travels—a process known as **propagation**—along the axon from the axon hillock to the axon terminals and into the synaptic end bulbs. When this signal reaches the end bulbs, it causes the release of a signaling molecule called a **neurotransmitter**.

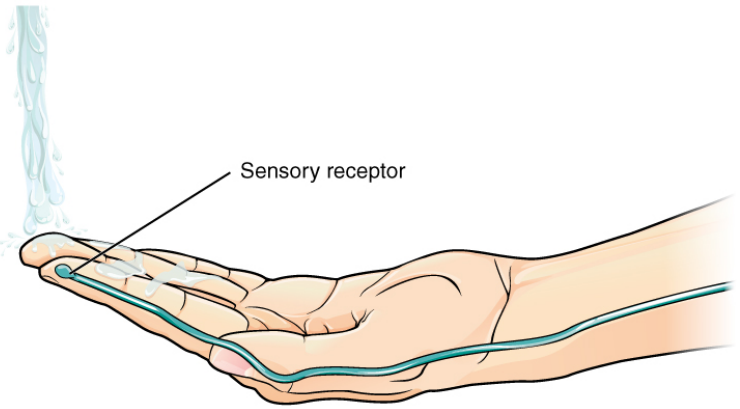


FIGURE 12.15 The Sensory Input Receptors in the skin sense the temperature of the water.

The neurotransmitter diffuses across the short distance of the synapse and binds to a receptor protein of the target neuron. When the molecular signal binds to the receptor, the cell membrane of the target neuron changes its electrical state and a new graded potential begins. If that graded potential is strong enough to reach threshold, the second neuron generates an action potential at its axon hillock. The target of this neuron is another neuron in the **thalamus** of the brain, the part of the CNS that acts as a relay for sensory information. At another synapse, neurotransmitter is released and binds to its receptor. The thalamus then sends the sensory information to the **cerebral cortex**, the outermost layer of gray matter in the brain, where conscious perception of that water temperature begins.

Within the cerebral cortex, information is processed among many neurons, integrating the stimulus of the water temperature with other sensory stimuli, with your emotional state (you just aren't ready to wake up; the bed is calling to you), memories (perhaps of the lab notes you have to study before a quiz). Finally, a plan is developed about what to do, whether that is to turn the temperature up, turn the whole shower off and go back to bed, or step into the shower. To do any of these things, the cerebral cortex has to send a command out to your body to move muscles (Figure 12.16).

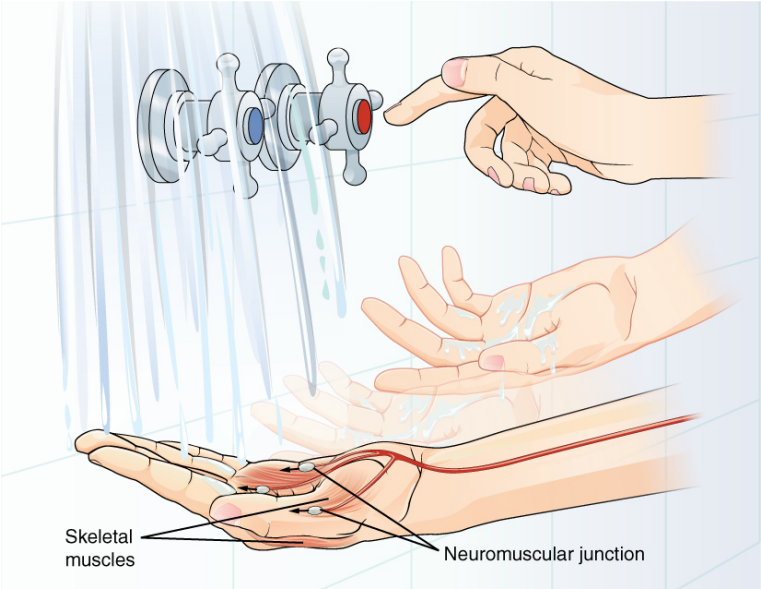


FIGURE 12.16 The Motor Response On the basis of the sensory input and the integration in the CNS, a motor response is formulated and executed.

A region of the cortex is specialized for sending signals down to the spinal cord for movement. The **upper motor neuron** is in this region, called the **precentral gyrus of the frontal cortex**, which has an axon that extends all the way down the spinal cord. At the level of the spinal cord at which this axon makes a synapse, a graded potential occurs in the cell membrane of a **lower motor neuron**. This second motor neuron is responsible for causing muscle fibers to contract. In the manner described in the chapter on muscle tissue, an action potential travels along the motor neuron axon into the periphery. The axon terminates on muscle fibers at the neuromuscular junction. Acetylcholine is released at this specialized synapse, which causes the muscle action potential to begin, following a large potential known as an end plate potential. When the lower motor neuron excites the muscle fiber, it contracts. All of this occurs in a fraction of a second, but this story is the basis of how the nervous system functions.

CAREER CONNECTION

Neurophysiologist

Understanding how the nervous system works could be a driving force in your career. Studying neurophysiology is a very rewarding path to follow. It means that there is a lot of work to do, but the rewards are worth the effort.

The career path of a research scientist can be straightforward: college, graduate school, postdoctoral research, academic research position at a university. A Bachelor's degree in science will get you started, and for neurophysiology that might be in biology, psychology, computer science, engineering, or neuroscience. But the real specialization comes in graduate school. There are many different programs out there to study the nervous system, not just neuroscience itself. Most graduate programs are doctoral, meaning that a Master's degree is not part of the work. These are usually considered five-year programs, with the first two years dedicated to course work and finding a research mentor, and the last three years dedicated to finding a research topic and pursuing that with a near single-mindedness. The research will usually result in a few publications in scientific journals, which will make up the bulk of a doctoral dissertation. After graduating with a Ph.D., researchers will go on to find specialized work called a postdoctoral fellowship within established labs. In this position, a researcher starts to establish their own research career with the hopes of finding an academic position at a research university.

Other options are available if you are interested in how the nervous system works. Especially for neurophysiology, a medical degree might be more suitable so you can learn about the clinical applications of neurophysiology and possibly work with human subjects. An academic career is not a necessity. Biotechnology firms are eager to find motivated scientists ready to tackle the tough questions about how the nervous system works so that therapeutic chemicals can be tested on some of the most challenging disorders such as Alzheimer's disease or Parkinson's disease, or spinal cord injury.

Others with a medical degree and a specialization in neuroscience go on to work directly with patients, diagnosing and treating mental disorders. You can do this as a psychiatrist, a neuropsychologist, a neuroscience nurse, or a neurodiagnostic technician, among other possible career paths.

12.4 The Action Potential

LEARNING OBJECTIVES

By the end of this section, you will be able to:

- Describe the components of the membrane that establish the resting membrane potential
- Describe the changes that occur to the membrane that result in the action potential

The functions of the nervous system—sensation, integration, and response—depend on the functions of the neurons underlying these pathways. To understand how neurons are able to communicate, it is necessary to describe the role of an **excitable membrane** in generating these signals. The basis of this communication is the action potential, which demonstrates how changes in the membrane can constitute a signal. Looking at the way these signals work in more variable circumstances involves a look at graded potentials, which will be covered in the next section.

Electrically Active Cell Membranes

Most cells in the body make use of charged particles, ions, to build up a charge across the cell membrane. Previously, this was shown to be a part of how muscle cells work. For skeletal muscles to contract, based on excitation–contraction coupling, requires input from a neuron. Both of the cells make use of the cell membrane to regulate ion movement between the extracellular fluid and cytosol.

As you learned in the chapter on cells, the cell membrane is primarily responsible for regulating what can cross the membrane and what stays on only one side. The cell membrane is a phospholipid bilayer, so only substances that can pass directly through the hydrophobic core can diffuse through unaided. Charged particles, which are hydrophilic by definition, cannot pass through the cell membrane without assistance (Figure 12.17). Transmembrane proteins, specifically channel proteins, make this possible. Several passive transport channels, as well as active transport pumps, are necessary to generate a transmembrane potential and an action potential. Of special interest is the carrier protein referred to as the sodium/potassium pump that moves sodium ions (Na^+) out of a cell and potassium ions (K^+) into a cell, thus regulating ion concentration on both sides of the cell membrane.

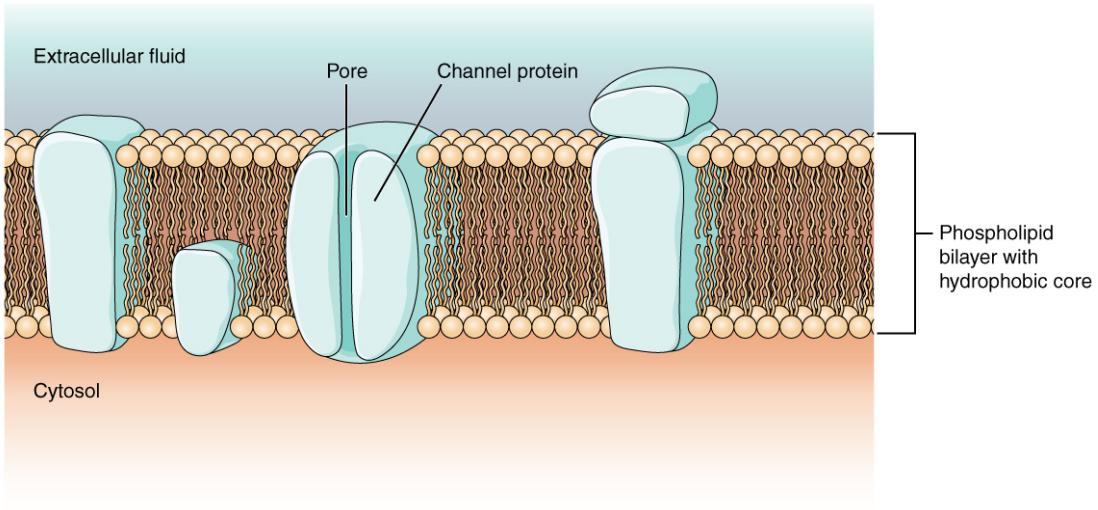


FIGURE 12.17 Cell Membrane and Transmembrane Proteins The cell membrane is composed of a phospholipid bilayer and has many transmembrane proteins, including different types of channel proteins that serve as ion channels.

The sodium/potassium pump requires energy in the form of adenosine triphosphate (ATP), so it is also referred to as an ATPase. As was explained in the cell chapter, the concentration of Na^+ is higher outside the cell than inside, and the concentration of K^+ is higher inside the cell than outside. That means that this pump is moving the ions against the concentration gradients for sodium and potassium, which is why it requires energy. In fact, the pump basically maintains those concentration gradients.

Ion channels are pores that allow specific charged particles to cross the membrane in response to an existing concentration gradient. Proteins are capable of spanning the cell membrane, including its hydrophobic core, and can interact with the charge of ions because of the varied properties of amino acids found within specific domains or regions of the protein channel. Hydrophobic amino acids are found in the domains that are apposed to the hydrocarbon tails of the phospholipids. Hydrophilic amino acids are exposed to the fluid environments of the extracellular fluid and cytosol. Additionally, the ions will interact with the hydrophilic amino acids, which will be selective for the charge of the ion. Channels for cations (positive ions) will have negatively charged side chains in the pore. Channels for anions (negative ions) will have positively charged side chains in the pore. This is called **electrochemical exclusion**, meaning that the channel pore is charge-specific.

Ion channels can also be specified by the diameter of the pore. The distance between the amino acids will be specific for the diameter of the ion when it dissociates from the water molecules surrounding it. Because of the surrounding water molecules, larger pores are not ideal for smaller ions because the water molecules will interact, by hydrogen bonds, more readily than the amino acid side chains. This is called **size exclusion**. Some ion channels are selective for charge but not necessarily for size, and thus are called a **nonspecific channel**. These nonspecific channels allow cations—particularly Na^+, K^+, and Ca^{2+}—to cross the membrane, but exclude anions.

Ion channels do not always freely allow ions to diffuse across the membrane. Some are opened by certain events, meaning the channels are **gated**. So another way that channels can be categorized is on the basis of how they are gated. Although these classes of ion channels are found primarily in the cells of nervous or muscular tissue, they also can be found in the cells of epithelial and connective tissues.

A **ligand-gated channel** opens because a signaling molecule, a ligand, binds to the extracellular region of the channel. This type of channel is also known as an **ionotropic receptor** because when the ligand, known as a neurotransmitter in the nervous system, binds to the protein, ions cross the membrane changing its charge (Figure 12.18).

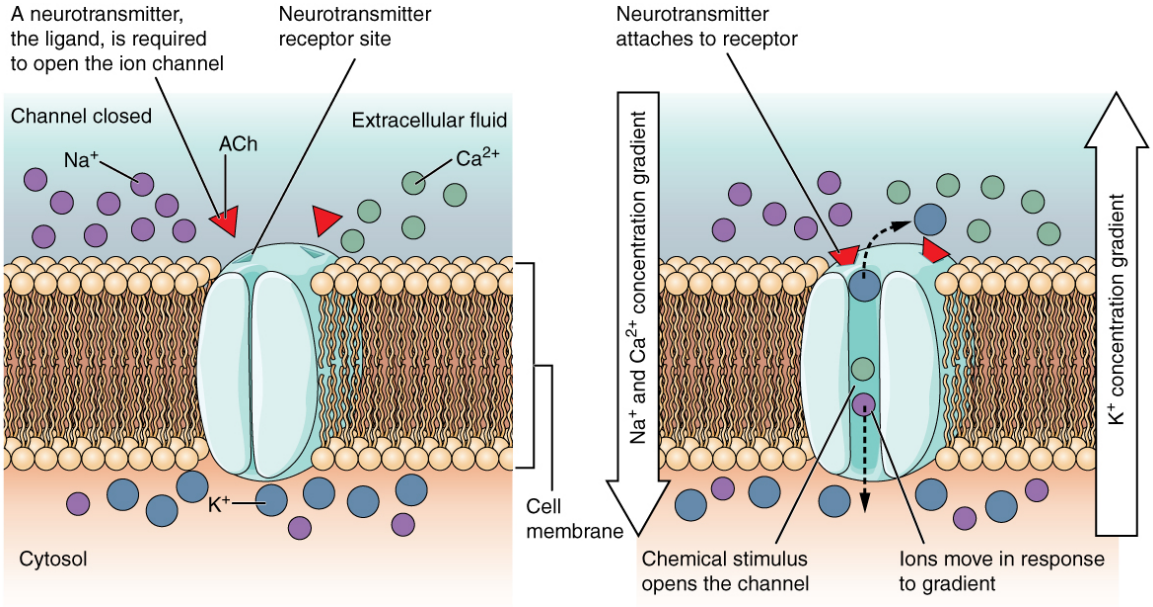


FIGURE 12.18 Ligand-Gated Channels When the ligand, in this case the neurotransmitter acetylcholine, binds to a specific location on the extracellular surface of the channel protein, the pore opens to allow select ions through. The ions, in this case, are cations of sodium, calcium, and potassium.

A **mechanically gated channel** opens because of a physical distortion of the cell membrane. Many channels associated with the sense of touch (somatosensation) are mechanically gated. For example, as pressure is applied to the skin, these channels open and allow ions to enter the cell. Similar to this type of channel would be the channel that opens on the basis of temperature changes, as in testing the water in the shower (Figure 12.19).

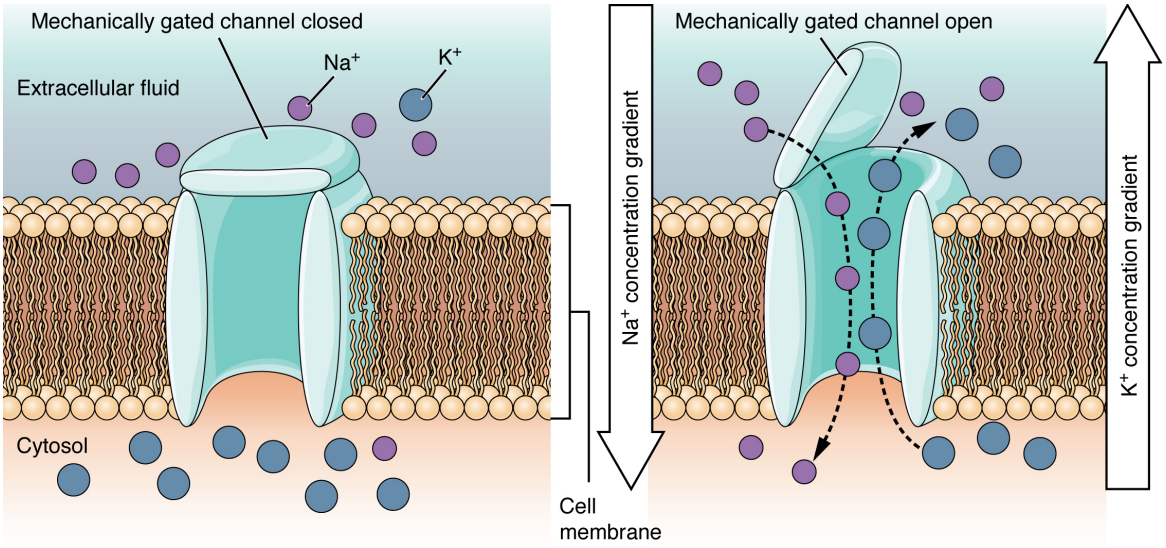


FIGURE 12.19 Mechanically Gated Channels When a mechanical change occurs in the surrounding tissue, such as pressure or touch, the channel is physically opened. Thermoreceptors work on a similar principle. When the local tissue temperature changes, the protein reacts by physically opening the channel.

A **voltage-gated channel** is a channel that responds to changes in the electrical properties of the membrane in which it is embedded. Normally, the inner portion of the membrane is at a negative voltage. When that voltage becomes less negative, the channel begins to allow ions to cross the membrane (Figure 12.20).

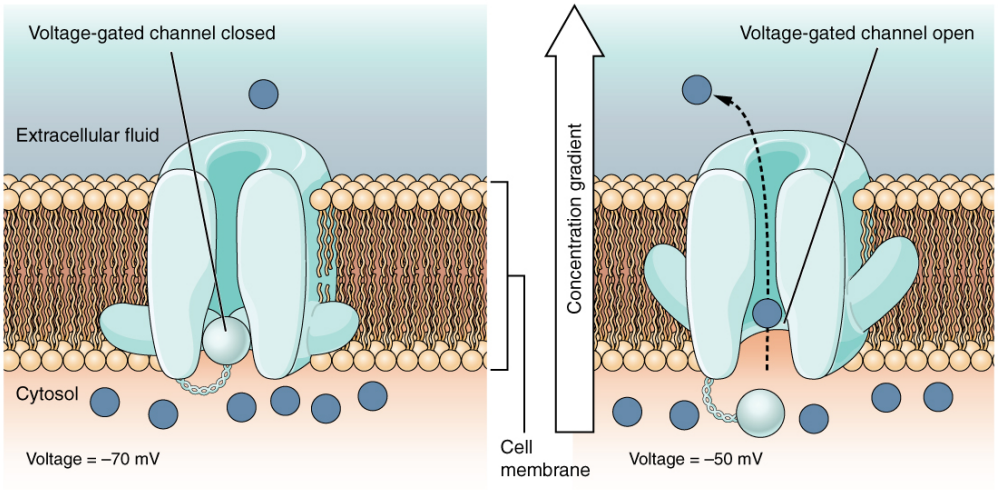


FIGURE 12.20 Voltage-Gated Channels Voltage-gated channels open when the transmembrane voltage changes around them. Amino acids in the structure of the protein are sensitive to charge and cause the pore to open to the selected ion.

A **leakage channel** is randomly gated, meaning that it opens and closes at random, hence the reference to leaking. There is no actual event that opens the channel; instead, it has an intrinsic rate of switching between the open and closed states. Leakage channels contribute to the resting transmembrane voltage of the excitable membrane (Figure 12.21).

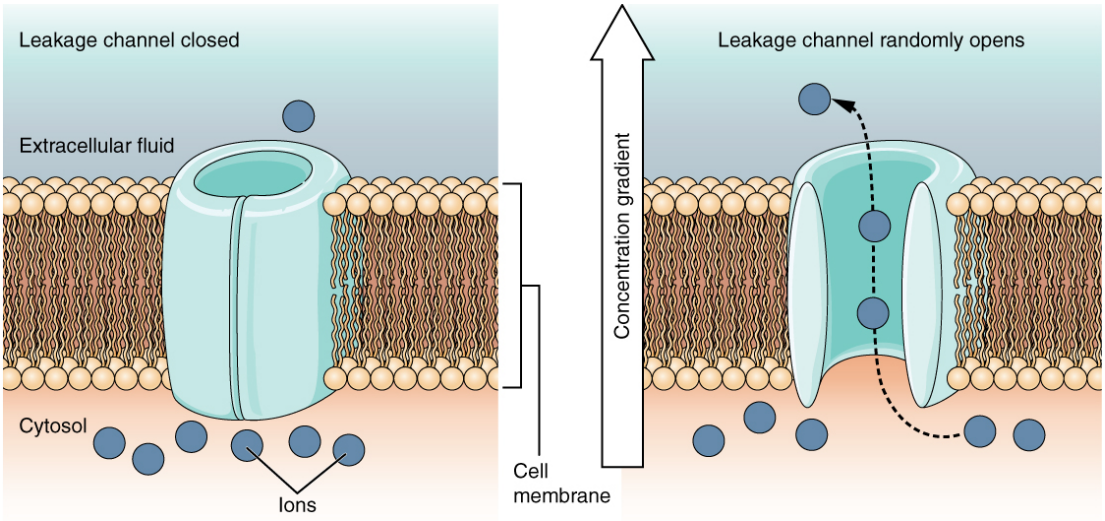


FIGURE 12.21 Leakage Channels In certain situations, ions need to move across the membrane randomly. The particular electrical properties of certain cells are modified by the presence of this type of channel.

The Membrane Potential

The electrical state of the cell membrane can have several variations. These are all variations in the **membrane potential**. A potential is a distribution of charge across the cell membrane, measured in millivolts (mV). The standard is to compare the inside of the cell relative to the outside, so the membrane potential is a value representing the charge on the intracellular side of the membrane based on the outside being zero, relatively speaking (Figure 12.22).

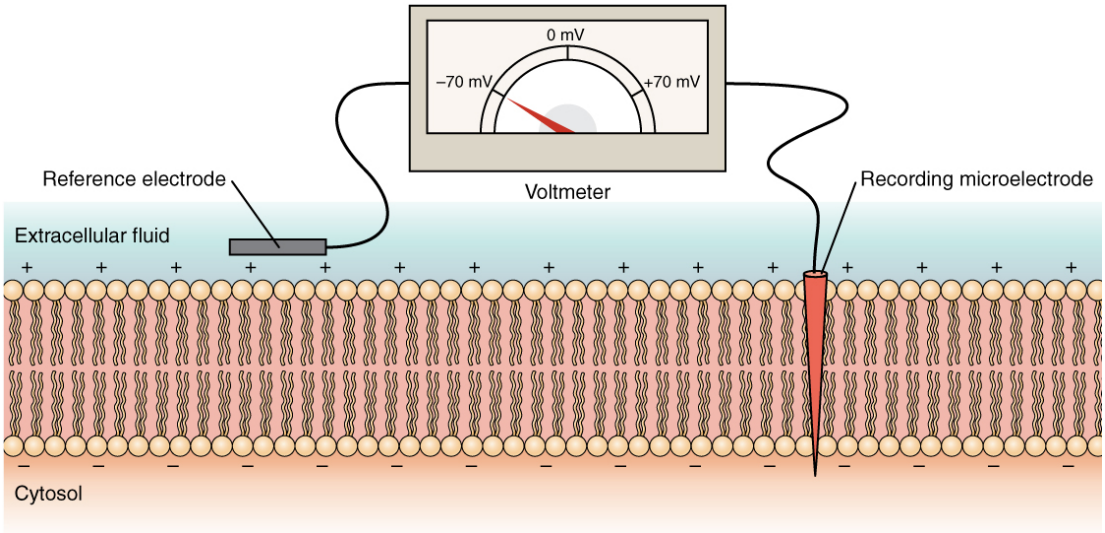


FIGURE 12.22 Measuring Charge across a Membrane with a Voltmeter A recording electrode is inserted into the cell and a reference electrode is outside the cell. By comparing the charge measured by these two electrodes, the transmembrane voltage is determined. It is conventional to express that value for the cytosol relative to the outside.

The concentration of ions in extracellular and intracellular fluids is largely balanced, with a net neutral charge. However, a slight difference in charge occurs right at the membrane surface, both internally and externally. It is the difference in this very limited region that has all the power in neurons (and muscle cells) to generate electrical signals, including action potentials.

Before these electrical signals can be described, the resting state of the membrane must be explained. When the cell is at rest, and the ion channels are closed (except for leakage channels which randomly open), ions are distributed across the membrane in a very predictable way. The concentration of Na^+ outside the cell is 10 times greater than the concentration inside. Also, the concentration of K^+ inside the cell is greater than outside. The cytosol contains a high concentration of anions, in the form of phosphate ions and negatively charged proteins.

Large anions are a component of the inner cell membrane, including specialized phospholipids and proteins associated with the inner leaflet of the membrane (leaflet is a term used for one side of the lipid bilayer membrane). The negative charge is localized in the large anions.

With the ions distributed across the membrane at these concentrations, the difference in charge is measured at -70 mV, the value described as the **resting membrane potential**. The exact value measured for the resting membrane potential varies between cells, but -70 mV is most commonly used as this value. This voltage would actually be much lower except for the contributions of some important proteins in the membrane. Leakage channels allow Na^+ to slowly move into the cell or K^+ to slowly move out, and the Na^+/K^+ pump restores them. This may appear to be a waste of energy, but each has a role in maintaining the membrane potential.

The Action Potential

Resting membrane potential describes the steady state of the cell, which is a dynamic process that is balanced by ion leakage and ion pumping. Without any outside influence, it will not change. To get an electrical signal started, the membrane potential has to change.

This starts with a channel opening for Na^+ in the membrane. Because the concentration of Na^+ is higher outside the cell than inside the cell by a factor of 10, ions will rush into the cell that are driven largely by the concentration gradient. Because sodium is a positively charged ion, it will change the relative voltage immediately inside the cell relative to immediately outside. The resting potential is the state of the membrane at a voltage of -70 mV, so the sodium cation entering the cell will cause it to become less negative. This is known as **depolarization**, meaning the membrane potential moves toward zero.

The concentration gradient for Na^+ is so strong that it will continue to enter the cell even after the membrane potential has become zero, so that the voltage immediately around the pore begins to become positive. The electrical gradient also plays a role, as negative proteins below the membrane attract the sodium ion. The membrane potential will reach +30 mV by the time sodium has entered the cell.

As the membrane potential reaches +30 mV, other voltage-gated channels are opening in the membrane. These channels are specific for the potassium ion. A concentration gradient acts on K^+, as well. As K^+ starts to leave the cell, taking a positive charge with it, the membrane potential begins to move back toward its resting voltage. This is called **repolarization**, meaning that the membrane voltage moves back toward the -70 mV value of the resting membrane potential.

Repolarization returns the membrane potential to the -70 mV value that indicates the resting potential, but it actually overshoots that value. Potassium ions reach equilibrium when the membrane voltage is below -70 mV, so a period of hyperpolarization occurs while the K^+ channels are open. Those K^+ channels are slightly delayed in closing, accounting for this short overshoot.

What has been described here is the action potential, which is presented as a graph of voltage over time in Figure 12.23. It is the electrical signal that nervous tissue generates for communication. The change in the membrane voltage from -70 mV at rest to +30 mV at the end of depolarization is a 100 mV change. That can also be written as a 0.1 V change. To put that value in perspective, think about a battery. An AA battery that you might find in a television remote has a voltage of 1.5 V, or a 9 V battery (the rectangular battery with two posts on one end) is, obviously, 9 V. The change seen in the action potential is one or two orders of magnitude less than the charge in these batteries. In fact, the membrane potential can be described as a battery. A charge is stored across the membrane that can be released under the correct conditions. A battery in your remote has stored a charge that is “released” when you push a button.

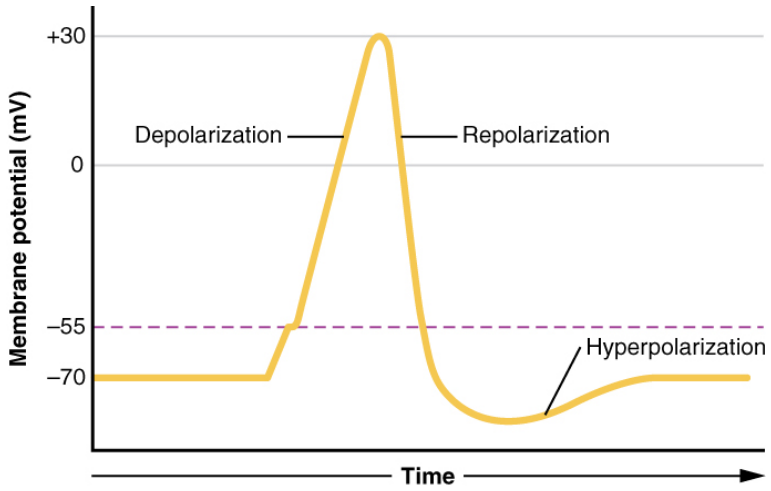


FIGURE 12.23 Graph of Action Potential Plotting voltage measured across the cell membrane against time, the action potential begins with depolarization, followed by repolarization, which goes past the resting potential into hyperpolarization, and finally the membrane returns to rest.

INTERACTIVE LINK

What happens across the membrane of an electrically active cell is a dynamic process that is hard to visualize with static images or through text descriptions. View this animation (http://openstax.org/l/dynamic1) to learn more about this process. What is the difference between the driving force for Na^+ and K^+? And what is similar about the movement of these two ions?

The question is, now, what initiates the action potential? The description above conveniently glosses over that point. But it is vital to understanding what is happening. The membrane potential will stay at the resting voltage until something changes. The description above just says that a Na^+ channel opens. Now, to say "a channel opens" does not mean that one individual transmembrane protein changes. Instead, it means that one kind of channel opens. There are a few different types of channels that allow Na^+ to cross the membrane. A ligand-gated Na^+ channel will open when a neurotransmitter binds to it and a mechanically gated Na^+ channel will open when a physical stimulus affects a sensory receptor (like pressure applied to the skin compresses a touch receptor). Whether it is a neurotransmitter binding to its receptor protein or a sensory stimulus activating a sensory receptor cell, some stimulus gets the process started. Sodium starts to enter the cell and the membrane becomes less negative.

A third type of channel that is an important part of depolarization in the action potential is the voltage-gated Na^+ channel. The channels that start depolarizing the membrane because of a stimulus help the cell to depolarize from -70 mV to -55 mV. Once the membrane reaches that voltage, the voltage-gated Na^+ channels open. This is what is known as the threshold. Any depolarization that does not change the membrane potential to -55 mV or higher will not reach threshold and thus will not result in an action potential. Also, any stimulus that depolarizes the membrane to -55 mV or beyond will cause a large number of channels to open and an action potential will be initiated.

Because of the threshold, the action potential can be likened to a digital event—it either happens or it does not. If the threshold is not reached, then no action potential occurs. If depolarization reaches -55 mV, then the action potential continues and runs all the way to +30 mV, at which K^+ causes repolarization, including the hyperpolarizing overshoot. Also, those changes are the same for every action potential, which means that once the threshold is reached, the exact same thing happens. A stronger stimulus, which might depolarize the membrane well past threshold, will not make a "bigger" action potential. Action potentials are "all or none." Either the membrane reaches the threshold and everything occurs as described above, or the membrane does not reach the threshold and nothing else happens. All action potentials peak at the same voltage (+30 mV), so one action potential is not bigger than another. Stronger stimuli will initiate multiple action potentials more quickly, but the individual signals are not bigger. Thus, for example, you will not feel a greater sensation of pain, or have a stronger muscle contraction, because of the size of the action potential because they are not different sizes.

As we have seen, the depolarization and repolarization of an action potential are dependent on two types of channels (the voltage-gated Na^+ channel and the voltage-gated K^+ channel). The voltage-gated Na^+ channel actually

has two gates. One is the **activation gate**, which opens when the membrane potential crosses -55 mV. The other gate is the **inactivation gate**, which closes after a specific period of time—on the order of a fraction of a millisecond. When a cell is at rest, the activation gate is closed and the inactivation gate is open. However, when the threshold is reached, the activation gate opens, allowing Na^+ to rush into the cell. Timed with the peak of depolarization, the inactivation gate closes. During repolarization, no more sodium can enter the cell. When the membrane potential passes -55 mV again, the activation gate closes. After that, the inactivation gate re-opens, making the channel ready to start the whole process over again.

The voltage-gated K^+ channel has only one gate, which is sensitive to a membrane voltage of -50 mV. However, it does not open as quickly as the voltage-gated Na^+ channel does. It might take a fraction of a millisecond for the channel to open once that voltage has been reached. The timing of this coincides exactly with when the Na^+ flow peaks, so voltage-gated K^+ channels open just as the voltage-gated Na^+ channels are being inactivated. As the membrane potential repolarizes and the voltage passes -50 mV again, the channel closes—again, with a little delay. Potassium continues to leave the cell for a short while and the membrane potential becomes more negative, resulting in the hyperpolarizing overshoot. Then the channel closes again and the membrane can return to the resting potential because of the ongoing activity of the non-gated channels and the Na^+/K^+ pump.

All of this takes place within approximately 2 milliseconds (Figure 12.24). While an action potential is in progress, another one cannot be initiated. That effect is referred to as the **refractory period**. There are two phases of the refractory period: the **absolute refractory period** and the **relative refractory period**. During the absolute phase, another action potential will not start. This is because of the inactivation gate of the voltage-gated Na^+ channel. Once that channel is back to its resting conformation (less than -55 mV), a new action potential could be started, but only by a stronger stimulus than the one that initiated the current action potential. This is because of the flow of K^+ out of the cell. Because that ion is rushing out, any Na^+ that tries to enter will not depolarize the cell, but will only keep the cell from hyperpolarizing.

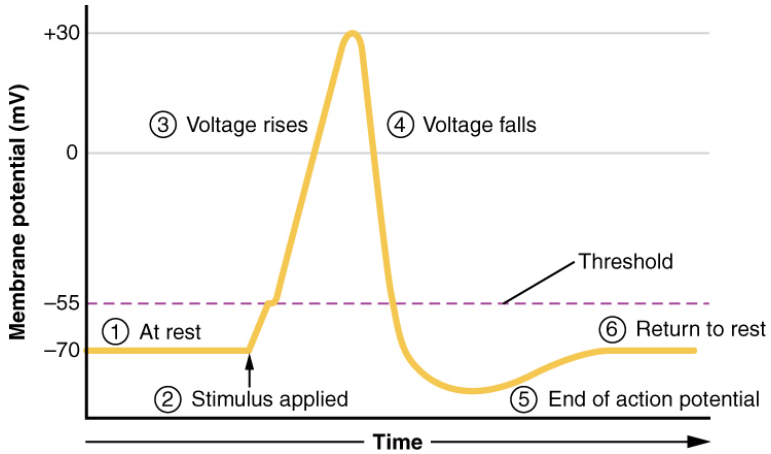


FIGURE 12.24 Stages of an Action Potential Plotting voltage measured across the cell membrane against time, the events of the action potential can be related to specific changes in the membrane voltage. (1) At rest, the membrane voltage is -70 mV. (2) The membrane begins to depolarize when an external stimulus is applied. (3) The membrane voltage begins a rapid rise toward +30 mV. (4) The membrane voltage starts to return to a negative value. (5) Repolarization continues past the resting membrane voltage, resulting in hyperpolarization. (6) The membrane voltage returns to the resting value shortly after hyperpolarization.

Propagation of the Action Potential

The action potential is initiated at the beginning of the axon, at what is called the initial segment. There is a high density of voltage-gated Na^+ channels so that rapid depolarization can take place here. Going down the length of the axon, the action potential is propagated because more voltage-gated Na^+ channels are opened as the depolarization spreads. This spreading occurs because Na^+ enters through the channel and moves along the inside of the cell membrane. As the Na^+ moves, or flows, a short distance along the cell membrane, its positive charge depolarizes a little more of the cell membrane. As that depolarization spreads, new voltage-gated Na^+ channels open and more ions rush into the cell, spreading the depolarization a little farther.

Because voltage-gated Na^+ channels are inactivated at the peak of the depolarization, they cannot be opened again for a brief time—the absolute refractory period. Because of this, depolarization spreading back toward previously opened channels has no effect. The action potential must propagate toward the axon terminals; as a result, the

polarity of the neuron is maintained, as mentioned above.

Propagation, as described above, applies to unmyelinated axons. When myelination is present, the action potential propagates differently. Sodium ions that enter the cell at the initial segment start to spread along the length of the axon segment, but there are no voltage-gated Na^+ channels until the first node of Ranvier. Because there is not constant opening of these channels along the axon segment, the depolarization spreads at an optimal speed. The distance between nodes is the optimal distance to keep the membrane still depolarized above threshold at the next node. As Na^+ spreads along the inside of the membrane of the axon segment, the charge starts to dissipate. If the node were any farther down the axon, that depolarization would have fallen off too much for voltage-gated Na^+ channels to be activated at the next node of Ranvier. If the nodes were any closer together, the speed of propagation would be slower.

Propagation along an unmyelinated axon is referred to as **continuous conduction**; along the length of a myelinated axon, it is **saltatory conduction**. Continuous conduction is slow because there are always voltage-gated Na^+ channels opening, and more and more Na^+ is rushing into the cell. Saltatory conduction is faster because the action potential basically jumps from one node to the next (saltare = “to leap”), and the new influx of Na^+ renews the depolarized membrane. Along with the myelination of the axon, the diameter of the axon can influence the speed of conduction. Much as water runs faster in a wide river than in a narrow creek, Na^+-based depolarization spreads faster down a wide axon than down a narrow one. This concept is known as **resistance** and is generally true for electrical wires or plumbing, just as it is true for axons, although the specific conditions are different at the scales of electrons or ions versus water in a river.

HOMEOSTATIC IMBALANCES

Potassium Concentration

Glial cells, especially astrocytes, are responsible for maintaining the chemical environment of the CNS tissue. The concentrations of ions in the extracellular fluid are the basis for how the membrane potential is established and changes in electrochemical signaling. If the balance of ions is upset, drastic outcomes are possible.

Normally the concentration of K^+ is higher inside the neuron than outside. After the repolarizing phase of the action potential, K^+ leakage channels and the Na^+/K^+ pump ensure that the ions return to their original locations. Following a stroke or other ischemic event, extracellular K^+ levels are elevated. The astrocytes in the area are equipped to clear excess K^+ to aid the pump. But when the level is far out of balance, the effects can be irreversible.

Astrocytes can become reactive in cases such as these, which impairs their ability to maintain the local chemical environment. The glial cells enlarge and their processes swell. They lose their K^+ buffering ability and the function of the pump is affected, or even reversed. One of the early signs of cell disease is this "leaking" of sodium ions into the body cells. This sodium/potassium imbalance negatively affects the internal chemistry of cells, preventing them from functioning normally.

INTERACTIVE LINK

Visit this site (http://openstax.org/l/neurolab) to see a virtual neurophysiology lab, and to observe electrophysiological processes in the nervous system, where scientists directly measure the electrical signals produced by neurons. Often, the action potentials occur so rapidly that watching a screen to see them occur is not helpful. A speaker is powered by the signals recorded from a neuron and it “pops” each time the neuron fires an action potential. These action potentials are firing so fast that it sounds like static on the radio. Electrophysiologists can recognize the patterns within that static to understand what is happening. Why is the leech model used for measuring the electrical activity of neurons instead of using humans?

12.5 Communication Between Neurons

LEARNING OBJECTIVES

By the end of this section, you will be able to:

- Explain the differences between the types of graded potentials
- Categorize the major neurotransmitters by chemical type and effect

The electrical changes taking place within a neuron, as described in the previous section, are similar to a light switch being turned on. A stimulus starts the depolarization, but the action potential runs on its own once a threshold has been reached. The question is now, "What flips the light switch on?" Temporary changes to the cell membrane voltage can result from neurons receiving information from the environment, or from the action of one neuron on another. These special types of potentials influence a neuron and determine whether an action potential will occur or not. Many of these transient signals originate at the synapse.

Graded Potentials

Local changes in the membrane potential are called graded potentials and are usually associated with the dendrites of a neuron. The amount of change in the membrane potential is determined by the size of the stimulus that causes it. In the example of testing the temperature of the shower, slightly warm water would only initiate a small change in a thermoreceptor, whereas hot water would cause a large amount of change in the membrane potential.

Graded potentials can be of two sorts, either they are depolarizing or hyperpolarizing (Figure 12.25). For a membrane at the resting potential, a graded potential represents a change in that voltage either above -70 mV or below -70 mV. Depolarizing graded potentials are often the result of Na^+ or Ca^{2+} entering the cell. Both of these ions have higher concentrations outside the cell than inside; because they have a positive charge, they will move into the cell causing it to become less negative relative to the outside. Hyperpolarizing graded potentials can be caused by K^+ leaving the cell or Cl^- entering the cell. If a positive charge moves out of a cell, the cell becomes more negative; if a negative charge enters the cell, the same thing happens.

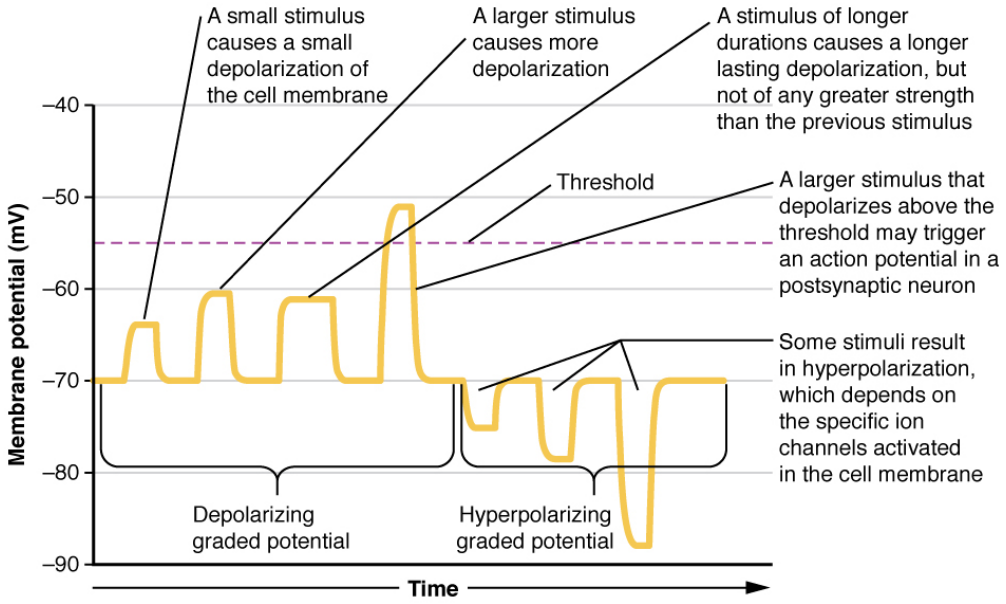


FIGURE 12.25 Graded Potentials Graded potentials are temporary changes in the membrane voltage, the characteristics of which depend on the size of the stimulus. Some types of stimuli cause depolarization of the membrane, whereas others cause hyperpolarization. It depends on the specific ion channels that are activated in the cell membrane.

Types of Graded Potentials

For the unipolar cells of sensory neurons—both those with free nerve endings and those within encapsulations—graded potentials develop in the dendrites that influence the generation of an action potential in the axon of the same cell. This is called a **generator potential**. For other sensory receptor cells, such as taste cells or photoreceptors of the retina, graded potentials in their membranes result in the release of neurotransmitters at synapses with sensory neurons. This is called a **receptor potential**.

A **postsynaptic potential (PSP)** is the graded potential in the dendrites of a neuron that is receiving synapses from other cells. Postsynaptic potentials can be depolarizing or hyperpolarizing. Depolarization in a postsynaptic potential is called an **excitatory postsynaptic potential (EPSP)** because it causes the membrane potential to move toward threshold. Hyperpolarization in a postsynaptic potential is an **inhibitory postsynaptic potential (IPSP)** because it causes the membrane potential to move away from threshold.

Summation

All types of graded potentials will result in small changes of either depolarization or hyperpolarization in the voltage of a membrane. These changes can lead to the neuron reaching threshold if the changes add together, or **summate**. The combined effects of different types of graded potentials are illustrated in Figure 12.26. If the total change in voltage in the membrane is a positive 15 mV, meaning that the membrane depolarizes from -70 mV to -55 mV, then the graded potentials will result in the membrane reaching threshold.

For receptor potentials, threshold is not a factor because the change in membrane potential for receptor cells directly causes neurotransmitter release. However, generator potentials can initiate action potentials in the sensory neuron axon, and postsynaptic potentials can initiate an action potential in the axon of other neurons. Graded potentials summate at a specific location at the beginning of the axon to initiate the action potential, namely the initial segment. For sensory neurons, which do not have a cell body between the dendrites and the axon, the initial segment is directly adjacent to the dendritic endings. For all other neurons, the axon hillock is essentially the initial segment of the axon, and it is where summation takes place. These locations have a high density of voltage-gated Na^+ channels that initiate the depolarizing phase of the action potential.

Summation can be spatial or temporal, meaning it can be the result of multiple graded potentials at different locations on the neuron, or all at the same place but separated in time. **Spatial summation** is related to associating the activity of multiple inputs to a neuron with each other. **Temporal summation** is the relationship of multiple action potentials from a single cell resulting in a significant change in the membrane potential. Spatial and temporal summation can act together, as well.

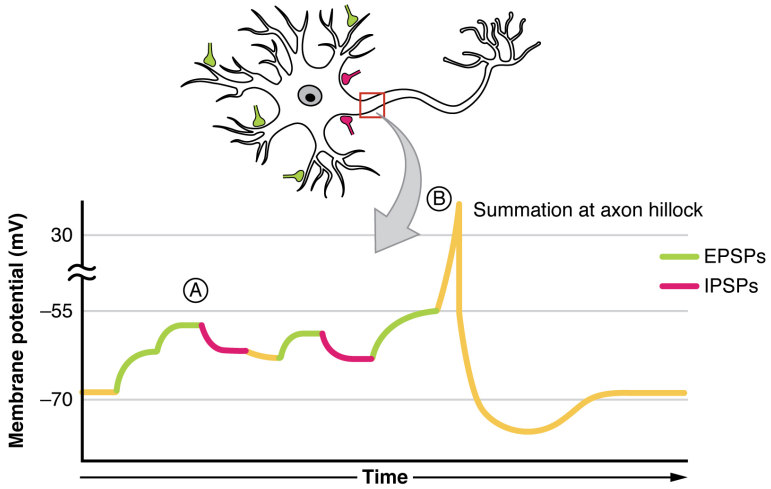


FIGURE 12.26 Postsynaptic Potential Summation The result of summation of postsynaptic potentials is the overall change in the membrane potential. At point A, several different excitatory postsynaptic potentials add up to a large depolarization. At point B, a mix of excitatory and inhibitory postsynaptic potentials result in a different end result for the membrane potential.

INTERACTIVE LINK

Watch this video (http://openstax.org/l/summation) to learn about summation. The process of converting electrical signals to chemical signals and back requires subtle changes that can result in transient increases or decreases in membrane voltage. To cause a lasting change in the target cell, multiple signals are usually added together, or summated. Does spatial summation have to happen all at once, or can the separate signals arrive on the postsynaptic neuron at slightly different times? Explain your answer.

Synapses

There are two types of connections between electrically active cells, chemical synapses and electrical synapses. In a **chemical synapse**, a chemical signal—namely, a neurotransmitter—is released from one cell and it affects the other cell. In an **electrical synapse**, there is a direct connection between the two cells so that ions can pass directly from one cell to the next. If one cell is depolarized in an electrical synapse, the joined cell also depolarizes because the ions pass between the cells. Chemical synapses involve the transmission of chemical information from one cell to the next. This section will concentrate on the chemical type of synapse.

An example of a chemical synapse is the neuromuscular junction (NMJ) described in the chapter on muscle tissue. In the nervous system, there are many more synapses that are essentially the same as the NMJ. All synapses have common characteristics, which can be summarized in this list:

- presynaptic element
- neurotransmitter (packaged in vesicles)
- synaptic cleft
- receptor proteins
- postsynaptic element
- neurotransmitter elimination or re-uptake

For the NMJ, these characteristics are as follows: the presynaptic element is the motor neuron's axon terminals, the neurotransmitter is acetylcholine, the synaptic cleft is the space between the cells where the neurotransmitter diffuses, the receptor protein is the nicotinic acetylcholine receptor, the postsynaptic element is the sarcolemma of the muscle cell, and the neurotransmitter is eliminated by acetylcholinesterase. Other synapses are similar to this, and the specifics are different, but they all contain the same characteristics.

Neurotransmitter Release

When an action potential reaches the axon terminals, voltage-gated Ca^{2+} channels in the membrane of the synaptic end bulb open. The concentration of Ca^{2+} increases inside the end bulb, and the Ca^{2+} ion associates with proteins in the outer surface of neurotransmitter vesicles. The Ca^{2+} facilitates the merging of the vesicle with the presynaptic membrane so that the neurotransmitter is released through exocytosis into the small gap between the cells, known as the **synaptic cleft**.

Once in the synaptic cleft, the neurotransmitter diffuses the short distance to the postsynaptic membrane and can interact with neurotransmitter receptors. Receptors are specific for the neurotransmitter, and the two fit together like a key and lock. One neurotransmitter binds to its receptor and will not bind to receptors for other neurotransmitters, making the binding a specific chemical event (Figure 12.27).

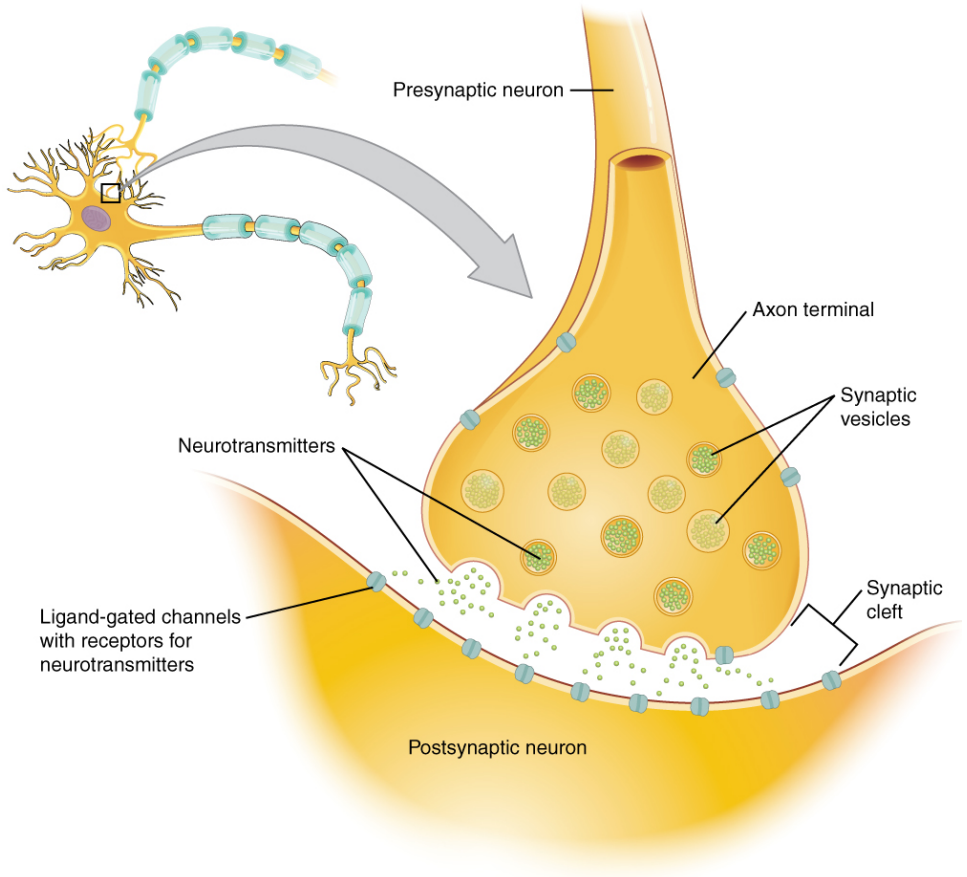


FIGURE 12.27 The Synapse The synapse is a connection between a neuron and its target cell (which is not necessarily a neuron). The presynaptic element is the synaptic end bulb of the axon where Ca^{2+} enters the bulb to cause vesicle fusion and neurotransmitter release. The neurotransmitter diffuses across the synaptic cleft to bind to its receptor. The neurotransmitter is cleared from the synapse either by enzymatic degradation, neuronal reuptake, or glial reuptake.

Neurotransmitter Systems

There are several systems of neurotransmitters that are found at various synapses in the nervous system. These groups refer to the chemicals that are the neurotransmitters, and within the groups are specific systems.

The first group, which is a neurotransmitter system of its own, is the **cholinergic system**. It is the system based on acetylcholine. This includes the NMJ as an example of a cholinergic synapse, but cholinergic synapses are found in other parts of the nervous system. They are in the autonomic nervous system, as well as distributed throughout the brain.

The cholinergic system has two types of receptors, the **nicotinic receptor** is found in the NMJ as well as other synapses. There is also an acetylcholine receptor known as the **muscarinic receptor**. Both of these receptors are named for drugs that interact with the receptor in addition to acetylcholine. Nicotine will bind to the nicotinic receptor and activate it similar to acetylcholine. Muscarine, a product of certain mushrooms, will bind to the muscarinic receptor. However, nicotine will not bind to the muscarinic receptor and muscarine will not bind to the nicotinic receptor.

Another group of neurotransmitters are amino acids. This includes glutamate (Glu), GABA (gamma-aminobutyric acid, a derivative of glutamate), and glycine (Gly). These amino acids have an amino group and a carboxyl group in their chemical structures. Glutamate is one of the 20 amino acids that are used to make proteins. Each amino acid neurotransmitter would be part of its own system, namely the glutamatergic, GABAergic, and glycinergic systems. They each have their own receptors and do not interact with each other. Amino acid neurotransmitters are eliminated from the synapse by reuptake. A pump in the cell membrane of the presynaptic element, or sometimes a neighboring glial cell, will clear the amino acid from the synaptic cleft so that it can be recycled, repackaged in vesicles, and released again.

Another class of neurotransmitter is the **biogenic amine**, a group of neurotransmitters that are enzymatically made from amino acids. They have amino groups in them, but no longer have carboxyl groups and are therefore no longer classified as amino acids. Serotonin is made from tryptophan. It is the basis of the serotonergic system, which has its own specific receptors. Serotonin is transported back into the presynaptic cell for repackaging.

Other biogenic amines are made from tyrosine, and include dopamine, norepinephrine, and epinephrine. Dopamine is part of its own system, the dopaminergic system, which has dopamine receptors. Dopamine is removed from the synapse by transport proteins in the presynaptic cell membrane. Norepinephrine and epinephrine belong to the adrenergic neurotransmitter system. The two molecules are very similar and bind to the same receptors, which are referred to as alpha and beta receptors. Norepinephrine and epinephrine are also transported back into the presynaptic cell. The chemical epinephrine (epi- = "on"; "-nephrine" = kidney) is also known as adrenaline (renal = "kidney"), and norepinephrine is sometimes referred to as noradrenaline. The adrenal gland produces epinephrine and norepinephrine to be released into the blood stream as hormones.

A **neuropeptide** is a neurotransmitter molecule made up of chains of amino acids connected by peptide bonds. This is what a protein is, but the term protein implies a certain length to the molecule. Some neuropeptides are quite short, such as met-enkephalin, which is five amino acids long. Others are long, such as beta-endorphin, which is 31 amino acids long. Neuropeptides are often released at synapses in combination with another neurotransmitter, and they often act as hormones in other systems of the body, such as vasoactive intestinal peptide (VIP) or substance P.

The effect of a neurotransmitter on the postsynaptic element is entirely dependent on the receptor protein. First, if there is no receptor protein in the membrane of the postsynaptic element, then the neurotransmitter has no effect. The depolarizing or hyperpolarizing effect is also dependent on the receptor. When acetylcholine binds to the nicotinic receptor, the postsynaptic cell is depolarized. This is because the receptor is a cation channel and positively charged Na^+ will rush into the cell. However, when acetylcholine binds to the muscarinic receptor, of which there are several variants, it might cause depolarization or hyperpolarization of the target cell.

The amino acid neurotransmitters, glutamate, glycine, and GABA, are almost exclusively associated with just one effect. Glutamate is considered an excitatory amino acid, but only because Glu receptors in the adult cause depolarization of the postsynaptic cell. Glycine and GABA are considered inhibitory amino acids, again because their receptors cause hyperpolarization.

The biogenic amines have mixed effects. For example, the dopamine receptors that are classified as D1 receptors are excitatory whereas D2-type receptors are inhibitory. Biogenic amine receptors and neuropeptide receptors can have even more complex effects because some may not directly affect the membrane potential, but rather have an effect on gene transcription or other metabolic processes in the neuron. The characteristics of the various neurotransmitter systems presented in this section are organized in Table 12.3.

The important thing to remember about neurotransmitters, and signaling chemicals in general, is that the effect is entirely dependent on the receptor. Neurotransmitters bind to one of two classes of receptors at the cell surface, ionotropic or metabotropic (Figure 12.28). Ionotropic receptors are ligand-gated ion channels, such as the nicotinic receptor for acetylcholine or the glycine receptor. A **metabotropic receptor** involves a complex of proteins that result in metabolic changes within the cell. The receptor complex includes the transmembrane receptor protein, a G protein, and an effector protein. The neurotransmitter, referred to as the first messenger, binds to the receptor protein on the extracellular surface of the cell, and the intracellular side of the protein initiates activity of the G protein. The **G protein** is a guanosine triphosphate (GTP) hydrolase that physically moves from the receptor protein to the effector protein to activate the latter. An **effector protein** is an enzyme that catalyzes the generation of a new molecule, which acts as the intracellular mediator of the signal that binds to the receptor. This intracellular mediator is called the second messenger.

Different receptors use different second messengers. Two common examples of second messengers are cyclic adenosine monophosphate (cAMP) and inositol triphosphate (IP_3). The enzyme adenylate cyclase (an example of an effector protein) makes cAMP, and phospholipase C is the enzyme that makes IP_3. Second messengers, after they are produced by the effector protein, cause metabolic changes within the cell. These changes are most likely the activation of other enzymes in the cell. In neurons, they often modify ion channels, either opening or closing them. These enzymes can also cause changes in the cell, such as the activation of genes in the nucleus, and therefore the increased synthesis of proteins. In neurons, these kinds of changes are often the basis of stronger connections

between cells at the synapse and may be the basis of learning and memory.

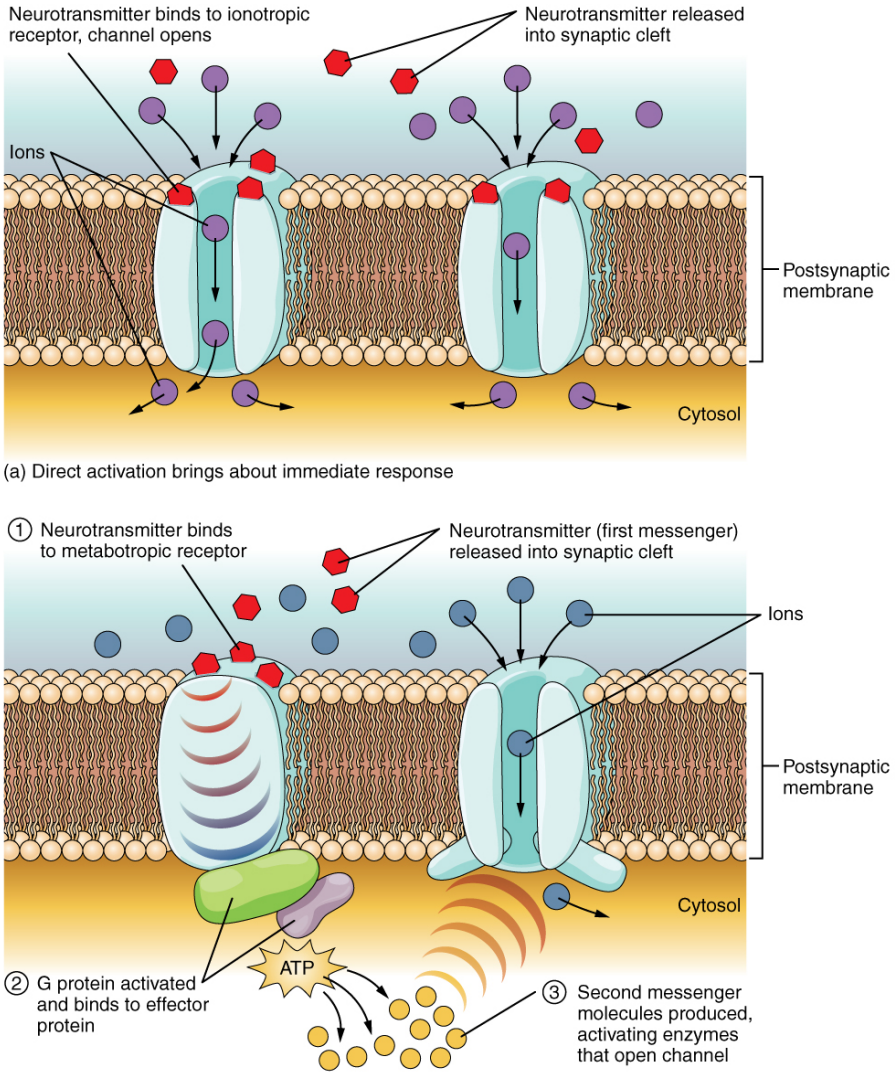


FIGURE 12.28 **Receptor Types** (a) An ionotropic receptor is a channel that opens when the neurotransmitter binds to it. (b) A metabotropic receptor is a complex that causes metabolic changes in the cell when the neurotransmitter binds to it (1). After binding, the G protein hydrolyzes ATP and moves to the effector protein (2). When the G protein contacts the effector protein, the latter is activated. In the case shown, the effector protein then acts on ATP to generate a second messenger, cAMP (3). The second messenger can then go on to cause changes in the neuron, such as opening or closing ion channels, metabolic changes, and changes in gene transcription.

INTERACTIVE LINK

Watch this video (http://openstax.org/l/neurotrans) to learn about the release of a neurotransmitter. The action potential reaches the end of the axon, called the axon terminal, and a chemical signal is released to tell the target cell to do something—either to initiate a new action potential, or to suppress that activity. In a very short space, the electrical signal of the action potential is changed into the chemical signal of a neurotransmitter and then back to electrical changes in the target cell membrane. What is the importance of voltage-gated calcium channels in the release of neurotransmitters?

Characteristics of Neurotransmitter Systems

System	Cholinergic	Amino acids	Biogenic amines	Neuropeptides
Neurotransmitters	Acetylcholine	Glutamate, glycine, GABA	Serotonin (5-HT), dopamine, norepinephrine, (epinephrine)	Met-enkephalin, beta-endorphin, VIP, Substance P, etc.
Receptors	Nicotinic and muscarinic receptors	Glu receptors, gly receptors, GABA receptors	5-HT receptors, D1 and D2 receptors, α-adrenergic and β-adrenergic receptors	Receptors are too numerous to list, but are specific to the peptides.
Elimination	Degradation by acetylcholinesterase	Reuptake by neurons or glia	Reuptake by neurons	Degradation by enzymes called peptidases
Postsynaptic effect	Nicotinic receptor causes depolarization. Muscarinic receptors can cause both depolarization or hyperpolarization depending on the subtype.	Glu receptors cause depolarization. Gly and GABA receptors cause hyperpolarization.	Depolarization or hyperpolarization depends on the specific receptor. For example, D1 receptors cause depolarization and D2 receptors cause hyperpolarization.	Depolarization or hyperpolarization depends on the specific receptor.

TABLE 12.3

Disorders of the...

Nervous System

The underlying cause of some neurodegenerative diseases, such as Alzheimer's and Parkinson's, appears to be related to proteins—specifically, to proteins behaving badly. One of the strongest theories of what causes Alzheimer's disease is based on the accumulation of beta-amyloid plaques, dense conglomerations of a protein that is not functioning correctly. Parkinson's disease is linked to an increase in a protein known as alpha-synuclein that is toxic to the cells of the substantia nigra nucleus in the midbrain.

For proteins to function correctly, they are dependent on their three-dimensional shape. The linear sequence of amino acids folds into a three-dimensional shape that is based on the interactions between and among those amino acids. When the folding is disturbed, and proteins take on a different shape, they stop functioning correctly. But the disease is not necessarily the result of functional loss of these proteins; rather, these altered proteins start to accumulate and may become toxic. For example, in Alzheimer's, the hallmark of the disease is the accumulation of these amyloid plaques in the cerebral cortex. The term coined to describe this sort of disease is "proteopathy" and it includes other diseases. Creutzfeld-Jacob disease, the human variant of the prion disease known as mad cow disease in the bovine, also involves the accumulation of amyloid plaques, similar to Alzheimer's. Diseases of other organ systems can fall into this group as well, such as cystic fibrosis or type 2 diabetes. Recognizing the relationship between these diseases has suggested new therapeutic possibilities. Interfering with the accumulation of the proteins, and possibly as early as their original production within the cell, may unlock new ways to alleviate these devastating diseases.

Key Terms

absolute refractory period time during an action period when another action potential cannot be generated because the voltage-gated Na^+ channel is inactivated

action potential change in voltage of a cell membrane in response to a stimulus that results in transmission of an electrical signal; unique to neurons and muscle fibers

activation gate part of the voltage-gated Na^+ channel that opens when the membrane voltage reaches threshold

astrocyte glial cell type of the CNS that provides support for neurons and maintains the blood-brain barrier

autonomic nervous system (ANS) functional division of the nervous system that is responsible for homeostatic reflexes that coordinate control of cardiac and smooth muscle, as well as glandular tissue

axon single process of the neuron that carries an electrical signal (action potential) away from the cell body toward a target cell

axon hillock tapering of the neuron cell body that gives rise to the axon

axon segment single stretch of the axon insulated by myelin and bounded by nodes of Ranvier at either end (except for the first, which is after the initial segment, and the last, which is followed by the axon terminal)

axon terminal end of the axon, where there are usually several branches extending toward the target cell

axoplasm cytoplasm of an axon, which is different in composition than the cytoplasm of the neuronal cell body

biogenic amine class of neurotransmitters that are enzymatically derived from amino acids but no longer contain a carboxyl group

bipolar shape of a neuron with two processes extending from the neuron cell body—the axon and one dendrite

blood-brain barrier (BBB) physiological barrier between the circulatory system and the central nervous system that establishes a privileged blood supply, restricting the flow of substances into the CNS

brain the large organ of the central nervous system composed of white and gray matter, contained within the cranium and continuous with the spinal cord

central nervous system (CNS) anatomical division of the nervous system located within the cranial and vertebral cavities, namely the brain and spinal cord

cerebral cortex outermost layer of gray matter in the brain, where conscious perception takes place

cerebrospinal fluid (CSF) circulatory medium within the CNS that is produced by ependymal cells in the choroid plexus filtering the blood

chemical synapse connection between two neurons, or between a neuron and its target, where a neurotransmitter diffuses across a very short distance

cholinergic system neurotransmitter system of acetylcholine, which includes its receptors and the enzyme acetylcholinesterase

choroid plexus specialized structure containing ependymal cells that line blood capillaries and filter blood to produce CSF in the four ventricles of the brain

continuous conduction slow propagation of an action potential along an unmyelinated axon owing to voltage-gated Na^+ channels located along the entire length of the cell membrane

dendrite one of many branchlike processes that extends from the neuron cell body and functions as a contact for incoming signals (synapses) from other neurons or sensory cells

depolarization change in a cell membrane potential from rest toward zero

effector protein enzyme that catalyzes the generation of a new molecule, which acts as the intracellular mediator of the signal that binds to the receptor

electrical synapse connection between two neurons, or any two electrically active cells, where ions flow directly through channels spanning their adjacent cell membranes

electrochemical exclusion principle of selectively allowing ions through a channel on the basis of their charge

enteric nervous system (ENS) neural tissue associated with the digestive system that is responsible for nervous control through autonomic connections

ependymal cell glial cell type in the CNS responsible for producing cerebrospinal fluid

excitable membrane cell membrane that regulates the movement of ions so that an electrical signal can be generated

excitatory postsynaptic potential (EPSP) graded potential in the postsynaptic membrane that is the result of depolarization and makes an action potential more likely to occur

G protein guanosine triphosphate (GTP) hydrolase

that physically moves from the receptor protein to the effector protein to activate the latter

ganglion localized collection of neuron cell bodies in the peripheral nervous system

gated property of a channel that determines how it opens under specific conditions, such as voltage change or physical deformation

generator potential graded potential from dendrites of a unipolar cell which generates the action potential in the initial segment of that cell's axon

glial cell one of the various types of neural tissue cells responsible for maintenance of the tissue, and largely responsible for supporting neurons

graded potential change in the membrane potential that varies in size, depending on the size of the stimulus that elicits it

gray matter regions of the nervous system containing cell bodies of neurons with few or no myelinated axons; actually may be more pink or tan in color, but called gray in contrast to white matter

inactivation gate part of a voltage-gated Na^+ channel that closes when the membrane potential reaches +30 mV

inhibitory postsynaptic potential (IPSP) graded potential in the postsynaptic membrane that is the result of hyperpolarization and makes an action potential less likely to occur

initial segment first part of the axon as it emerges from the axon hillock, where the electrical signals known as action potentials are generated

integration nervous system function that combines sensory perceptions and higher cognitive functions (memories, learning, emotion, etc.) to produce a response

ionotropic receptor neurotransmitter receptor that acts as an ion channel gate, and opens by the binding of the neurotransmitter

leakage channel ion channel that opens randomly and is not gated to a specific event, also known as a non-gated channel

ligand-gated channels another name for an ionotropic receptor for which a neurotransmitter is the ligand

lower motor neuron second neuron in the motor command pathway that is directly connected to the skeletal muscle

mechanically gated channel ion channel that opens when a physical event directly affects the structure of the protein

membrane potential distribution of charge across the cell membrane, based on the charges of ions

metabotropic receptor neurotransmitter receptor that involves a complex of proteins that cause metabolic changes in a cell

microglia glial cell type in the CNS that serves as the resident component of the immune system

multipolar shape of a neuron that has multiple processes—the axon and two or more dendrites

muscarinic receptor type of acetylcholine receptor protein that is characterized by also binding to muscarine and is a metabotropic receptor

myelin lipid-rich insulating substance surrounding the axons of many neurons, allowing for faster transmission of electrical signals

myelin sheath lipid-rich layer of insulation that surrounds an axon, formed by oligodendrocytes in the CNS and Schwann cells in the PNS; facilitates the transmission of electrical signals

nerve cord-like bundle of axons located in the peripheral nervous system that transmits sensory input and response output to and from the central nervous system

neuron neural tissue cell that is primarily responsible for generating and propagating electrical signals into, within, and out of the nervous system

neuropeptide neurotransmitter type that includes protein molecules and shorter chains of amino acids

neurotransmitter chemical signal that is released from the synaptic end bulb of a neuron to cause a change in the target cell

nicotinic receptor type of acetylcholine receptor protein that is characterized by also binding to nicotine and is an ionotropic receptor

node of Ranvier gap between two myelinated regions of an axon, allowing for strengthening of the electrical signal as it propagates down the axon

nonspecific channel channel that is not specific to one ion over another, such as a nonspecific cation channel that allows any positively charged ion across the membrane

nucleus in the nervous system, a localized collection of neuron cell bodies that are functionally related; a "center" of neural function

oligodendrocyte glial cell type in the CNS that provides the myelin insulation for axons in tracts

peripheral nervous system (PNS) anatomical division of the nervous system that is largely outside the cranial and vertebral cavities, namely all parts except the brain and spinal cord

postsynaptic potential (PSP) graded potential in the postsynaptic membrane caused by the binding of neurotransmitter to protein receptors

precentral gyrus of the frontal cortex region of the cerebral cortex responsible for generating motor commands, where the upper motor neuron cell body is located

process in cells, an extension of a cell body; in the case of neurons, this includes the axon and dendrites

propagation movement of an action potential along the length of an axon

receptor potential graded potential in a specialized sensory cell that directly causes the release of neurotransmitter without an intervening action potential

refractory period time after the initiation of an action potential when another action potential cannot be generated

relative refractory period time during the refractory period when a new action potential can only be initiated by a stronger stimulus than the current action potential because voltage-gated K^+ channels are not closed

repolarization return of the membrane potential to its normally negative voltage at the end of the action potential

resistance property of an axon that relates to the ability of particles to diffuse through the cytoplasm; this is inversely proportional to the fiber diameter

response nervous system function that causes a target tissue (muscle or gland) to produce an event as a consequence to stimuli

resting membrane potential the difference in voltage measured across a cell membrane under steady-state conditions, typically -70 mV

saltatory conduction quick propagation of the action potential along a myelinated axon owing to voltage-gated Na^+ channels being present only at the nodes of Ranvier

satellite cell glial cell type in the PNS that provides support for neurons in the ganglia

Schwann cell glial cell type in the PNS that provides the myelin insulation for axons in nerves

sensation nervous system function that receives information from the environment and translates it into the electrical signals of nervous tissue

size exclusion principle of selectively allowing ions through a channel on the basis of their relative size

soma in neurons, that portion of the cell that contains the nucleus; the cell body, as opposed to the cell processes (axons and dendrites)

somatic nervous system (SNS) functional division of the nervous system that is concerned with conscious perception, voluntary movement, and skeletal muscle reflexes

spatial summation combination of graded potentials across the neuronal cell membrane caused by signals from separate presynaptic elements that add up to initiate an action potential

spinal cord organ of the central nervous system found within the vertebral cavity and connected with the periphery through spinal nerves; mediates reflex behaviors

stimulus an event in the external or internal environment that registers as activity in a sensory neuron

summate to add together, as in the cumulative change in postsynaptic potentials toward reaching threshold in the membrane, either across a span of the membrane or over a certain amount of time

synapse narrow junction across which a chemical signal passes from neuron to the next, initiating a new electrical signal in the target cell

synaptic cleft small gap between cells in a chemical synapse where neurotransmitter diffuses from the presynaptic element to the postsynaptic element

synaptic end bulb swelling at the end of an axon where neurotransmitter molecules are released onto a target cell across a synapse

temporal summation combination of graded potentials at the same location on a neuron resulting in a strong signal from one input

thalamus region of the central nervous system that acts as a relay for sensory pathways

thermoreceptor type of sensory receptor capable of transducing temperature stimuli into neural action potentials

threshold membrane voltage at which an action potential is initiated

tract bundle of axons in the central nervous system having the same function and point of origin

unipolar shape of a neuron which has only one process that includes both the axon and dendrite

upper motor neuron first neuron in the motor command pathway with its cell body in the cerebral cortex that synapses on the lower motor neuron in the spinal cord

ventricle central cavity within the brain where CSF is produced and circulates

voltage-gated channel ion channel that opens because of a change in the charge distributed across the membrane where it is located

white matter regions of the nervous system containing mostly myelinated axons, making the tissue appear white because of the high lipid content of myelin

Chapter Review

12.1 Basic Structure and Function of the Nervous System

The nervous system can be separated into divisions on the basis of anatomy and physiology. The anatomical divisions are the central and peripheral nervous systems. The CNS is the brain and spinal cord. The PNS is everything else. Functionally, the nervous system can be divided into those regions that are responsible for sensation, those that are responsible for integration, and those that are responsible for generating responses. All of these functional areas are found in both the central and peripheral anatomy.

Considering the anatomical regions of the nervous system, there are specific names for the structures within each division. A localized collection of neuron cell bodies is referred to as a nucleus in the CNS and as a ganglion in the PNS. A bundle of axons is referred to as a tract in the CNS and as a nerve in the PNS. Whereas nuclei and ganglia are specifically in the central or peripheral divisions, axons can cross the boundary between the two. A single axon can be part of a nerve and a tract. The name for that specific structure depends on its location.

Nervous tissue can also be described as gray matter and white matter on the basis of its appearance in unstained tissue. These descriptions are more often used in the CNS. Gray matter is where nuclei are found and white matter is where tracts are found. In the PNS, ganglia are basically gray matter and nerves are white matter.

The nervous system can also be divided on the basis of how it controls the body. The somatic nervous system (SNS) is responsible for functions that result in moving skeletal muscles. Any sensory or integrative functions that result in the movement of skeletal muscle would be considered somatic. The autonomic nervous system (ANS) is responsible for functions that affect cardiac or smooth muscle tissue, or that cause glands to produce their secretions. Autonomic functions are distributed between central and peripheral regions of the nervous system. The sensations that lead to autonomic functions can be the same sensations that are part of initiating somatic responses. Somatic and autonomic integrative functions may overlap as well.

A special division of the nervous system is the enteric nervous system, which is responsible for controlling the digestive organs. Parts of the autonomic nervous system overlap with the enteric nervous system. The enteric nervous system is exclusively found in the periphery because it is the nervous tissue in the organs of the digestive system.

12.2 Nervous Tissue

Nervous tissue contains two major cell types, neurons and glial cells. Neurons are the cells responsible for communication through electrical signals. Glial cells are supporting cells, maintaining the environment around the neurons.

Neurons are polarized cells, based on the flow of electrical signals along their membrane. Signals are received at the dendrites, are passed along the cell body, and propagate along the axon towards the target, which may be another neuron, muscle tissue, or a gland. Many axons are insulated by a lipid-rich substance called myelin. Specific types of glial cells provide this insulation.

Several types of glial cells are found in the nervous system, and they can be categorized by the anatomical division in which they are found. In the CNS, astrocytes, oligodendrocytes, microglia, and ependymal cells are found. Astrocytes are important for maintaining the chemical environment around the neuron and are crucial for regulating the blood-brain barrier. Oligodendrocytes are the myelinating glia in the CNS. Microglia act as phagocytes and play a role in immune surveillance. Ependymal cells are responsible for filtering the blood to produce cerebrospinal fluid, which is a circulatory fluid that performs some of the functions of blood in the brain and spinal cord because of the BBB. In the PNS, satellite cells are supporting cells for the neurons, and Schwann cells insulate peripheral axons.

12.3 The Function of Nervous Tissue

Sensation starts with the activation of a sensory ending, such as the thermoreceptor in the skin sensing the temperature of the water. The sensory endings in the skin initiate an electrical signal that travels along the sensory axon within a nerve into the spinal cord, where it synapses with a neuron in the gray matter of the spinal cord. The temperature information represented in that electrical signal is passed to the next neuron by a chemical signal that diffuses across the small gap of the synapse and initiates a new electrical signal in the target cell. That signal travels through the sensory pathway to the brain, passing through the thalamus, where conscious perception of the water temperature is made possible by the cerebral cortex. Following integration of that information with other cognitive processes and sensory

information, the brain sends a command back down to the spinal cord to initiate a motor response by controlling a skeletal muscle. The motor pathway is composed of two cells, the upper motor neuron and the lower motor neuron. The upper motor neuron has its cell body in the cerebral cortex and synapses on a cell in the gray matter of the spinal cord. The lower motor neuron is that cell in the gray matter of the spinal cord and its axon extends into the periphery where it synapses with a skeletal muscle in a neuromuscular junction.

12.4 The Action Potential

The nervous system is characterized by electrical signals that are sent from one area to another. Whether those areas are close or very far apart, the signal must travel along an axon. The basis of the electrical signal is the controlled distribution of ions across the membrane. Transmembrane ion channels regulate when ions can move in or out of the cell, so that a precise signal is generated. This signal is the action potential which has a very characteristic shape based on voltage changes across the membrane in a given time period.

The membrane is normally at rest with established Na^+ and K^+ concentrations on either side. A stimulus will start the depolarization of the membrane, and voltage-gated channels will result in further depolarization followed by repolarization of the membrane. A slight overshoot of hyperpolarization marks the end of the action potential. While an action potential is in progress, another cannot be generated under the same conditions. While the voltage-gated Na^+ channel is inactivated, absolutely no action potentials can be generated. Once that channel has returned to its resting state, a new action potential is possible, but it must be started by a relatively stronger stimulus to overcome the K^+ leaving the cell.

The action potential travels down the axon as voltage-gated ion channels are opened by the spreading depolarization. In unmyelinated axons, this happens in a continuous fashion because there are voltage-gated channels throughout the membrane. In myelinated axons, propagation is described as saltatory because voltage-gated channels are only found at the nodes of Ranvier and the electrical events seem to “jump” from one node to the next. Saltatory conduction is faster than continuous conduction, meaning that myelinated axons propagate their signals faster. The diameter of the axon also makes a difference as ions diffusing within the cell have less resistance in a wider space.

12.5 Communication Between Neurons

The basis of the electrical signal within a neuron is the action potential that propagates down the axon. For a neuron to generate an action potential, it needs to receive input from another source, either another neuron or a sensory stimulus. That input will result in opening ion channels in the neuron, resulting in a graded potential based on the strength of the stimulus. Graded potentials can be depolarizing or hyperpolarizing and can summate to affect the probability of the neuron reaching threshold.

Graded potentials can be the result of sensory stimuli. If the sensory stimulus is received by the dendrites of a unipolar sensory neuron, such as the sensory neuron ending in the skin, the graded potential is called a generator potential because it can directly generate the action potential in the initial segment of the axon. If the sensory stimulus is received by a specialized sensory receptor cell, the graded potential is called a receptor potential. Graded potentials produced by interactions between neurons at synapses are called postsynaptic potentials (PSPs). A depolarizing graded potential at a synapse is called an excitatory PSP, and a hyperpolarizing graded potential at a synapse is called an inhibitory PSP.

Synapses are the contacts between neurons, which can either be chemical or electrical in nature. Chemical synapses are far more common. At a chemical synapse, neurotransmitter is released from the presynaptic element and diffuses across the synaptic cleft. The neurotransmitter binds to a receptor protein and causes a change in the postsynaptic membrane (the PSP). The neurotransmitter must be inactivated or removed from the synaptic cleft so that the stimulus is limited in time.

The particular characteristics of a synapse vary based on the neurotransmitter system produced by that neuron. The cholinergic system is found at the neuromuscular junction and in certain places within the nervous system. Amino acids, such as glutamate, glycine, and gamma-aminobutyric acid (GABA) are used as neurotransmitters. Other neurotransmitters are the result of amino acids being enzymatically changed, as in the biogenic amines, or being covalently bonded together, as in the neuropeptides.

Interactive Link Questions

1. In 2003, the Nobel Prize in Physiology or Medicine was awarded to Paul C. Lauterbur and Sir Peter Mansfield for discoveries related to magnetic resonance imaging (MRI). This is a tool to see the structures of the body (not just the nervous system) that depends on magnetic fields associated with certain atomic nuclei. The utility of this technique in the nervous system is that fat tissue and water appear as different shades between black and white. Because white matter is fatty (from myelin) and gray matter is not, they can be easily distinguished in MRI images. Visit the Nobel Prize website (http://openstax.org/l/nobel_2) to play an interactive game that demonstrates the use of this technology and compares it with other types of imaging technologies. Also, the results from an MRI session are compared with images obtained from x-ray or computed tomography. How do the imaging techniques shown in this game indicate the separation of white and gray matter compared with the freshly dissected tissue shown earlier?
2. Visit this site (http://openstax.org/l/troublewstairs) to read about a woman that notices that her daughter is having trouble walking up the stairs. This leads to the discovery of a hereditary condition that affects the brain and spinal cord. The electromyography and MRI tests indicated deficiencies in the spinal cord and cerebellum, both of which are responsible for controlling coordinated movements. To what functional division of the nervous system would these structures belong?
3. The neurons are dynamic cells with the ability to make a vast number of connections and to respond incredibly quickly to stimuli and to initiate movements based on those stimuli. They are the focus of intense research as failures in physiology can lead to devastating illnesses. Why are neurons only found in animals? Why wouldn't they be helpful for plants or microorganisms?
4. View the University of Michigan Webscope (http://openstax.org/l/nervefiber) to see an electron micrograph of a cross-section of a myelinated nerve fiber. The axon contains microtubules and neurofilaments, bounded by a plasma membrane known as the axolemma. Outside the plasma membrane of the axon is the myelin sheath, which is composed of the tightly wrapped plasma membrane of a Schwann cell. What aspects of the cells in this image react with the stain that makes them the deep, dark, black color, such as the multiple layers that are the myelin sheath?
5. What happens across the membrane of an electrically active cell is a dynamic process that is hard to visualize with static images or through text descriptions. View this animation (http://openstax.org/l/dynamic1) to really understand the process. What is the difference between the driving force for Na^+ and K^+? And what is similar about the movement of these two ions?
6. Visit this site (http://openstax.org/l/neurolab) to see a virtual neurophysiology lab, and to observe electrophysiological processes in the nervous system, where scientists directly measure the electrical signals produced by neurons. Often, the action potentials occur so rapidly that watching a screen to see them occur is not helpful. A speaker is powered by the signals recorded from a neuron and it "pops" each time the neuron fires an action potential. These action potentials are firing so fast that it sounds like static on the radio. Electrophysiologists can recognize the patterns within that static to understand what is happening. Why is the leech model used for measuring the electrical activity of neurons instead of using humans?
7. Watch this video (http://openstax.org/l/summation) to learn about summation. The process of converting electrical signals to chemical signals and back requires subtle changes that can result in transient increases or decreases in membrane voltage. To cause a lasting change in the target cell, multiple signals are usually added together, or summated. Does spatial summation have to happen all at once, or can the separate signals arrive on the postsynaptic neuron at slightly different times? Explain your answer.
8. Watch this video (http://openstax.org/l/neurotrans) to learn about the release of a neurotransmitter. The action potential reaches the end of the axon, called the axon terminal, and a chemical signal is released to tell the target cell to do something, either initiate a new action potential, or to suppress that activity. In a very short space, the electrical signal of the action potential is changed into the chemical signal of a neurotransmitter, and then back to electrical changes in the target cell membrane. What is the importance of voltage-gated calcium channels in the release of neurotransmitters?

Review Questions

9. Which of the following cavities contains a component of the central nervous system?
a. abdominal
b. pelvic
c. cranial
d. thoracic

10. Which structure predominates in the white matter of the brain?
a. myelinated axons
b. neuronal cell bodies
c. ganglia of the parasympathetic nerves
d. bundles of dendrites from the enteric nervous system

11. Which part of a neuron transmits an electrical signal to a target cell?
a. dendrites
b. soma
c. cell body
d. axon

12. Which term describes a bundle of axons in the peripheral nervous system?
a. nucleus
b. ganglion
c. tract
d. nerve

13. Which functional division of the nervous system would be responsible for the physiological changes seen during exercise (e.g., increased heart rate and sweating)?
a. somatic
b. autonomic
c. enteric
d. central

14. What type of glial cell provides myelin for the axons in a tract?
a. oligodendrocyte
b. astrocyte
c. Schwann cell
d. satellite cell

15. Which part of a neuron contains the nucleus?
a. dendrite
b. soma
c. axon
d. synaptic end bulb

16. Which of the following substances is least able to cross the blood-brain barrier?
a. water
b. sodium ions
c. glucose
d. white blood cells

17. What type of glial cell is the resident macrophage behind the blood-brain barrier?
a. microglia
b. astrocyte
c. Schwann cell
d. satellite cell

18. What two types of macromolecules are the main components of myelin?
a. carbohydrates and lipids
b. proteins and nucleic acids
c. lipids and proteins
d. carbohydrates and nucleic acids

19. If a thermoreceptor is sensitive to temperature sensations, what would a chemoreceptor be sensitive to?
a. light
b. sound
c. molecules
d. vibration

20. Which of these locations is where the greatest level of integration is taking place in the example of testing the temperature of the shower?
a. skeletal muscle
b. spinal cord
c. thalamus
d. cerebral cortex

21. How long does all the signaling through the sensory pathway, within the central nervous system, and through the motor command pathway take?
a. 1 to 2 minutes
b. 1 to 2 seconds
c. fraction of a second
d. varies with graded potential

22. What is the target of an upper motor neuron?
a. cerebral cortex
b. lower motor neuron
c. skeletal muscle
d. thalamus

23. What ion enters a neuron causing depolarization of the cell membrane?
   a. sodium
   b. chloride
   c. potassium
   d. phosphate

24. Voltage-gated Na^+ channels open upon reaching what state?
   a. resting potential
   b. threshold
   c. repolarization
   d. overshoot

25. What does a ligand-gated channel require in order to open?
   a. increase in concentration of Na^+ ions
   b. binding of a neurotransmitter
   c. increase in concentration of K^+ ions
   d. depolarization of the membrane

26. What does a mechanically gated channel respond to?
   a. physical stimulus
   b. chemical stimulus
   c. increase in resistance
   d. decrease in resistance

27. Which of the following voltages would most likely be measured during the relative refractory period?
   a. +30 mV
   b. 0 mV
   c. -45 mV
   d. -80 mv

28. Which of the following is probably going to propagate an action potential fastest?
   a. a thin, unmyelinated axon
   b. a thin, myelinated axon
   c. a thick, unmyelinated axon
   d. a thick, myelinated axon

29. How much of a change in the membrane potential is necessary for the summation of postsynaptic potentials to result in an action potential being generated?
   a. +30 mV
   b. +15 mV
   c. +10 mV
   d. -15 mV

30. A channel opens on a postsynaptic membrane that causes a negative ion to enter the cell. What type of graded potential is this?
   a. depolarizing
   b. repolarizing
   c. hyperpolarizing
   d. non-polarizing

31. What neurotransmitter is released at the neuromuscular junction?
   a. norepinephrine
   b. serotonin
   c. dopamine
   d. acetylcholine

32. What type of receptor requires an effector protein to initiate a signal?
   a. biogenic amine
   b. ionotropic receptor
   c. cholinergic system
   d. metabotropic receptor

33. Which of the following neurotransmitters is associated with inhibition exclusively?
   a. GABA
   b. acetylcholine
   c. glutamate
   d. norepinephrine

Critical Thinking Questions

34. What responses are generated by the nervous system when you run on a treadmill? Include an example of each type of tissue that is under nervous system control.

35. When eating food, what anatomical and functional divisions of the nervous system are involved in the perceptual experience?

36. Multiple sclerosis is a demyelinating disease affecting the central nervous system. What type of cell would be the most likely target of this disease? Why?

37. Which type of neuron, based on its shape, is best suited for relaying information directly from one neuron to another? Explain why.

38. Sensory fibers, or pathways, are referred to as "afferent." Motor fibers, or pathways, are referred to as "efferent." What can you infer about the meaning of these two terms (afferent and efferent) in a structural or anatomical context?

39. If a person has a motor disorder and cannot move their arm voluntarily, but their muscles have tone, which motor neuron—upper or lower—is probably affected? Explain why.

40. What does it mean for an action potential to be an "all or none" event?

41. The conscious perception of pain is often delayed because of the time it takes for the sensations to reach the cerebral cortex. Why would this be the case based on propagation of the axon potential?

42. If a postsynaptic cell has synapses from five different cells, and three cause EPSPs and two of them cause IPSPs, give an example of a series of depolarizations and hyperpolarizations that would result in the neuron reaching threshold.

43. Why is the receptor the important element determining the effect a neurotransmitter has on a target cell?

CHAPTER 13
Anatomy of the Nervous System

Figure 13.1 **Human Nervous System** The ability to balance like an acrobat combines functions throughout the nervous system. The central and peripheral divisions coordinate control of the body using the senses of balance, body position, and touch on the soles of the feet. (credit: Rhett Sutphin)

CHAPTER OBJECTIVES

After studying this chapter, you will be able to:

- Relate the developmental processes of the embryonic nervous system to the adult structures
- Name the major regions of the adult nervous system
- Locate regions of the cerebral cortex on the basis of anatomical landmarks common to all human brains
- Describe the regions of the spinal cord in cross-section
- List the cranial nerves in order of anatomical location and provide the central and peripheral connections
- List the spinal nerves by vertebral region and by which nerve plexus each supplies

INTRODUCTION The nervous system is responsible for controlling much of the body, both through somatic (voluntary) and autonomic (involuntary) functions. The structures of the nervous system must be described in detail to understand how many of these functions are possible. There is a physiological concept known as localization of function that states that certain structures are specifically responsible for prescribed functions. It is an underlying concept in all of anatomy and physiology, but the nervous system illustrates the concept very well.

Fresh, unstained nervous tissue can be described as gray or white matter, and within those two types of tissue it can be very hard to see any detail. However, as specific regions and structures have been described, they were related to specific functions. Understanding these structures and the functions they perform requires a detailed description of the anatomy of the nervous system, delving deep into what the central and peripheral structures are.

The place to start this study of the nervous system is the beginning of the individual human life, within the womb. The embryonic development of the nervous system allows for a simple framework on which progressively more complicated structures can be built. With this framework in place, a thorough investigation of the nervous system is possible.

13.1 The Embryologic Perspective

LEARNING OBJECTIVES

By the end of this section, you will be able to:

- Describe the growth and differentiation of the neural tube
- Relate the different stages of development to the adult structures of the central nervous system
- Explain the expansion of the ventricular system of the adult brain from the central canal of the neural tube
- Describe the connections of the diencephalon and cerebellum on the basis of patterns of embryonic development

The brain is a complex organ composed of gray parts and white matter, which can be hard to distinguish. Starting from an embryologic perspective allows you to understand more easily how the parts relate to each other. The embryonic nervous system begins as a very simple structure—essentially just a straight line, which then gets increasingly complex. Looking at the development of the nervous system with a couple of early snapshots makes it easier to understand the whole complex system.

Many structures that appear to be adjacent in the adult brain are not connected, and the connections that exist may seem arbitrary. But there is an underlying order to the system that comes from how different parts develop. By following the developmental pattern, it is possible to learn what the major regions of the nervous system are.

The Neural Tube

To begin, a sperm cell and an egg cell fuse to become a fertilized egg. The fertilized egg cell, or zygote, starts dividing to generate the cells that make up an entire organism. Sixteen days after fertilization, the developing embryo's cells belong to one of three germ layers that give rise to the different tissues in the body. The endoderm, or inner tissue, is responsible for generating the lining tissues of various spaces within the body, such as the mucosae of the digestive and respiratory systems. The mesoderm, or middle tissue, gives rise to most of the muscle and connective tissues. Finally the ectoderm, or outer tissue, develops into the integumentary system (the skin) and the nervous system. It is probably not difficult to see that the outer tissue of the embryo becomes the outer covering of the body. But how is it responsible for the nervous system?

As the embryo develops, a portion of the ectoderm differentiates into a specialized region of neuroectoderm, which is the precursor for the tissue of the nervous system. Molecular signals induce cells in this region to differentiate into the neuroepithelium, forming a **neural plate**. The cells then begin to change shape, causing the tissue to buckle and fold inward (Figure 13.2). A **neural groove** forms, visible as a line along the dorsal surface of the embryo. The ridge-like edge on either side of the neural groove is referred as the **neural fold**. As the neural folds come together and converge, the underlying structure forms into a tube just beneath the ectoderm called the **neural tube**. Cells from the neural folds then separate from the ectoderm to form a cluster of cells referred to as the **neural crest**, which runs lateral to the neural tube. The neural crest migrates away from the nascent, or embryonic, central nervous system (CNS) that will form along the neural groove and develops into several parts of the peripheral nervous system (PNS), including the enteric nervous tissue. Many tissues that are not part of the nervous system also arise from the neural crest, such as craniofacial cartilage and bone, and melanocytes.

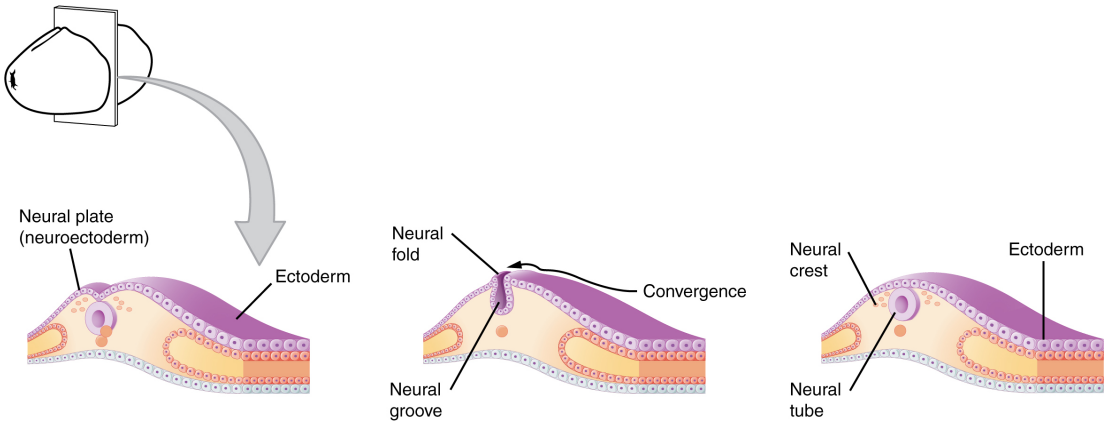


FIGURE 13.2 Early Embryonic Development of Nervous System The neuroectoderm begins to fold inward to form the neural groove.

As the two sides of the neural groove converge, they form the neural tube, which lies beneath the ectoderm. The anterior end of the neural tube will develop into the brain, and the posterior portion will become the spinal cord. The neural crest develops into peripheral structures.

At this point, the early nervous system is a simple, hollow tube. It runs from the anterior end of the embryo to the posterior end. Beginning at 25 days, the anterior end develops into the brain, and the posterior portion becomes the spinal cord. This is the most basic arrangement of tissue in the nervous system, and it gives rise to the more complex structures by the fourth week of development.

Primary Vesicles

As the anterior end of the neural tube starts to develop into the brain, it undergoes a couple of enlargements; the result is the production of sac-like vesicles. Similar to a child's balloon animal, the long, straight neural tube begins to take on a new shape. Three vesicles form at the first stage, which are called **primary vesicles**. These vesicles are given names that are based on Greek words, the main root word being *enkephalon*, which means "brain" (en- = "inside"; kephalon = "head"). The prefix to each generally corresponds to its position along the length of the developing nervous system.

The **prosencephalon** (pros- = "in front") is the forward-most vesicle, and the term can be loosely translated to mean **forebrain**. The **mesencephalon** (mes- = "middle") is the next vesicle, which can be called the **midbrain**. The third vesicle at this stage is the **rhombencephalon**. The first part of this word is also the root of the word rhombus, which is a geometrical figure with four sides of equal length (a square is a rhombus with 90° angles). Whereas prosencephalon and mesencephalon translate into the English words forebrain and midbrain, there is not a word for "four-sided-figure-brain." However, the third vesicle can be called the **hindbrain**. One way of thinking about how the brain is arranged is to use these three regions—forebrain, midbrain, and hindbrain—which are based on the primary vesicle stage of development (Figure 13.3**a**).

Secondary Vesicles

The brain continues to develop, and the vesicles differentiate further (see Figure 13.3**b**). The three primary vesicles become five **secondary vesicles**. The prosencephalon enlarges into two new vesicles called the **telencephalon** and the **diencephalon**. The telecephalon will become the cerebrum. The diencephalon gives rise to several adult structures; two that will be important are the thalamus and the hypothalamus. In the embryonic diencephalon, a structure known as the eye cup develops, which will eventually become the retina, the nervous tissue of the eye called the retina. This is a rare example of nervous tissue developing as part of the CNS structures in the embryo, but becoming a peripheral structure in the fully formed nervous system.

The mesencephalon does not differentiate into any finer divisions. The midbrain is an established region of the brain at the primary vesicle stage of development and remains that way. The rest of the brain develops around it and constitutes a large percentage of the mass of the brain. Dividing the brain into forebrain, midbrain, and hindbrain is useful in considering its developmental pattern, but the midbrain is a small proportion of the entire brain, relatively speaking.

The rhombencephalon develops into the **metencephalon** and **myelencephalon**. The metencephalon corresponds to the adult structure known as the pons and also gives rise to the cerebellum. The cerebellum (from the Latin meaning "little brain") accounts for about 10 percent of the mass of the brain and is an important structure in itself. The most significant connection between the cerebellum and the rest of the brain is at the pons, because the pons and cerebellum develop out of the same vesicle. The myelencephalon corresponds to the adult structure known as the medulla oblongata. The structures that come from the mesencephalon and rhombencephalon, except for the cerebellum, are collectively considered the **brain stem**, which specifically includes the midbrain, pons, and medulla.

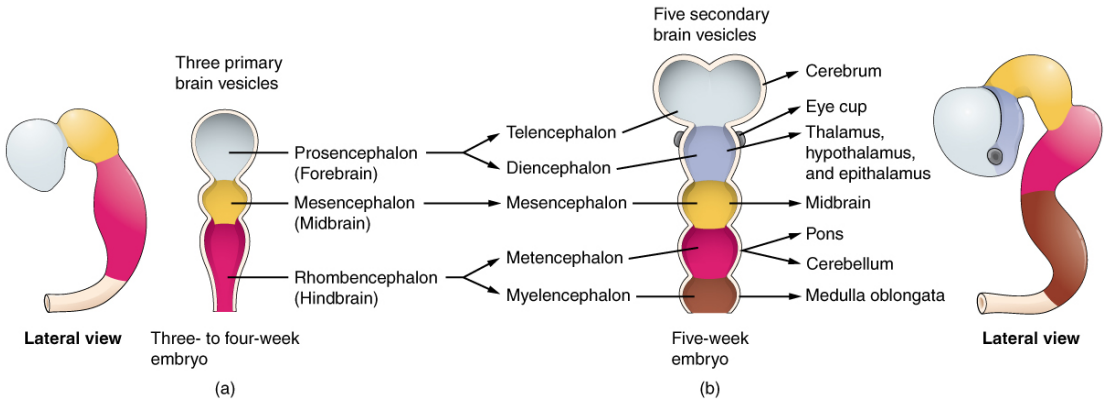


FIGURE 13.3 Primary and Secondary Vesicle Stages of Development The embryonic brain develops complexity through enlargements of the neural tube called vesicles; (a) The primary vesicle stage has three regions, and (b) the secondary vesicle stage has five regions.

INTERACTIVE LINK

Watch this animation (http://openstax.org/l/braindevel) to examine the development of the brain, starting with the neural tube. As the anterior end of the neural tube develops, it enlarges into the primary vesicles that establish the forebrain, midbrain, and hindbrain. Those structures continue to develop throughout the rest of embryonic development and into adolescence. They are the basis of the structure of the fully developed adult brain. How would you describe the difference in the relative sizes of the three regions of the brain when comparing the early (25th embryonic day) brain and the adult brain?

Spinal Cord Development

While the brain is developing from the anterior neural tube, the spinal cord is developing from the posterior neural tube. However, its structure does not differ from the basic layout of the neural tube. It is a long, straight cord with a small, hollow space down the center. The neural tube is defined in terms of its anterior versus posterior portions, but it also has a dorsal–ventral dimension. As the neural tube separates from the rest of the ectoderm, the side closest to the surface is dorsal, and the deeper side is ventral.

As the spinal cord develops, the cells making up the wall of the neural tube proliferate and differentiate into the neurons and glia of the spinal cord. The dorsal tissues will be associated with sensory functions, and the ventral tissues will be associated with motor functions.

Relating Embryonic Development to the Adult Brain

Embryonic development can help in understanding the structure of the adult brain because it establishes a framework on which more complex structures can be built. First, the neural tube establishes the anterior–posterior dimension of the nervous system, which is called the **neuraxis**. The embryonic nervous system in mammals can be said to have a standard arrangement. Humans (and other primates, to some degree) make this complicated by standing up and walking on two legs. The anterior–posterior dimension of the neuraxis overlays the superior–inferior dimension of the body. However, there is a major curve between the brain stem and forebrain, which is called the **cephalic flexure**. Because of this, the neuraxis starts in an inferior position—the end of the spinal cord—and ends in an anterior position, the front of the cerebrum. If this is confusing, just imagine a four-legged animal standing up on two legs. Without the flexure in the brain stem, and at the top of the neck, that animal would be looking straight up instead of straight in front (Figure 13.4).

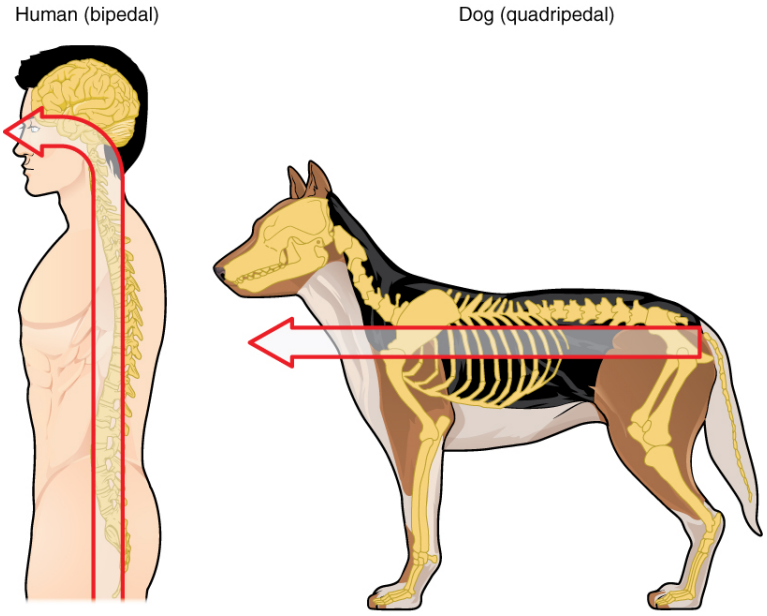


FIGURE 13.4 Human Neuraxis The mammalian nervous system is arranged with the neural tube running along an anterior to posterior axis, from nose to tail for a four-legged animal like a dog. Humans, as two-legged animals, have a bend in the neuraxis between the brain stem and the diencephalon, along with a bend in the neck, so that the eyes and the face are oriented forward.

In summary, the primary vesicles help to establish the basic regions of the nervous system: forebrain, midbrain, and hindbrain. These divisions are useful in certain situations, but they are not equivalent regions. The midbrain is small compared with the hindbrain and particularly the forebrain. The secondary vesicles go on to establish the major regions of the adult nervous system that will be followed in this text. The telencephalon is the cerebrum, which is the major portion of the human brain. The diencephalon continues to be referred to by this Greek name, because there is no better term for it (dia- = "through"). The diencephalon is between the cerebrum and the rest of the nervous system and can be described as the region through which all projections have to pass between the cerebrum and everything else. The brain stem includes the midbrain, pons, and medulla, which correspond to the mesencephalon, metencephalon, and myelencephalon. The cerebellum, being a large portion of the brain, is considered a separate region. Table 13.1 connects the different stages of development to the adult structures of the CNS.

One other benefit of considering embryonic development is that certain connections are more obvious because of how these adult structures are related. The retina, which began as part of the diencephalon, is primarily connected to the diencephalon. The eyes are just inferior to the anterior-most part of the cerebrum, but the optic nerve extends back to the thalamus as the optic tract, with branches into a region of the hypothalamus. There is also a connection of the optic tract to the midbrain, but the mesencephalon is adjacent to the diencephalon, so that is not difficult to imagine. The cerebellum originates out of the metencephalon, and its largest white matter connection is to the pons, also from the metencephalon. There are connections between the cerebellum and both the medulla and midbrain, which are adjacent structures in the secondary vesicle stage of development. In the adult brain, the cerebellum seems close to the cerebrum, but there is no direct connection between them.

Another aspect of the adult CNS structures that relates to embryonic development is the ventricles—open spaces within the CNS where cerebrospinal fluid circulates. They are the remnant of the hollow center of the neural tube. The four ventricles and the tubular spaces associated with them can be linked back to the hollow center of the embryonic brain (see Table 13.1).

Stages of Embryonic Development

Neural tube	Primary vesicle stage	Secondary vesicle stage	Adult structures	Ventricles
Anterior neural tube	Prosencephalon	Telencephalon	Cerebrum	Lateral ventricles
Anterior neural tube	Prosencephalon	Diencephalon	Diencephalon	Third ventricle
Anterior neural tube	Mesencephalon	Mesencephalon	Midbrain	Cerebral aqueduct
Anterior neural tube	Rhombencephalon	Metencephalon	Pons cerebellum	Fourth ventricle
Anterior neural tube	Rhombencephalon	Myelencephalon	Medulla	Fourth ventricle
Posterior neural tube			Spinal cord	Central canal

TABLE 13.1

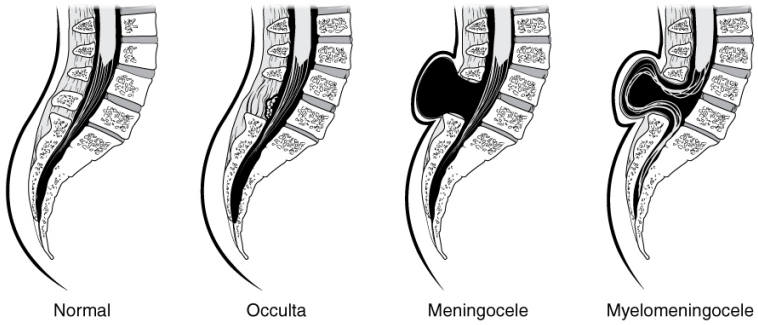
Disorders of the...

Nervous System

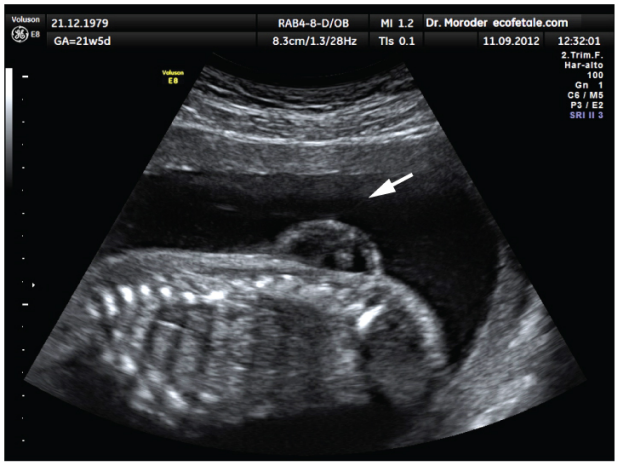
Early formation of the nervous system depends on the formation of the neural tube. A groove forms along the dorsal surface of the embryo, which becomes deeper until its edges meet and close off to form the tube. If this fails to happen, especially in the posterior region where the spinal cord forms, a developmental defect called spina bifida occurs. The closing of the neural tube is important for more than just the proper formation of the nervous system. The surrounding tissues are dependent on the correct development of the tube. The connective tissues surrounding the CNS can be involved as well.

There are three classes of this disorder: occulta, meningocele, and myelomeningocele (Figure 13.5). The first type, spina bifida occulta, is the mildest because the vertebral bones do not fully surround the spinal cord, but the spinal cord itself is not affected. No functional differences may be noticed, which is what the word occulta means; it is hidden spina bifida. The other two types both involve the formation of a cyst—a fluid-filled sac of the connective tissues that cover the spinal cord called the meninges. “Meningocele” means that the meninges protrude through the spinal column but nerves may not be involved and few symptoms are present, though complications may arise later in life. “Myelomeningocele” means that the meninges protrude and spinal nerves are involved, and therefore severe neurological symptoms can be present.

Often surgery to close the opening or to remove the cyst is necessary. The earlier that surgery can be performed, the better the chances of controlling or limiting further damage or infection at the opening. For many children with meningocele, surgery will alleviate the pain, although they may experience some functional loss. Because the myelomeningocele form of spina bifida involves more extensive damage to the nervous tissue, neurological damage may persist, but symptoms can often be handled. Complications of the spinal cord may present later in life, but overall life expectancy is not reduced.



(a)



(b)

FIGURE 13.5 **Spinal Bifida** (a) Spina bifida is a birth defect of the spinal cord caused when the neural tube does not completely close, but the rest of development continues. The result is the emergence of meninges and neural tissue through the vertebral column. (b) Fetal myelomeningocele is evident in this ultrasound taken at 21 weeks.

INTERACTIVE LINK

Watch this video (http://openstax.org/l/whitematter) to learn about the white matter in the cerebrum that develops during childhood and adolescence. This is a composite of MRI images taken of the brains of people from 5 years of age through 20 years of age, demonstrating how the cerebrum changes. As the color changes to blue, the ratio of gray matter to white matter changes. The caption for the video describes it as "less gray matter," which is another way of saying "more white matter." If the brain does not finish developing until approximately 20 years of age, can teenagers be held responsible for behaving badly?

13.2 The Central Nervous System

LEARNING OBJECTIVES

By the end of this section, you will be able to:

- Name the major regions of the adult brain
- Describe the connections between the cerebrum and brain stem through the diencephalon, and from those regions into the spinal cord
- Recognize the complex connections within the subcortical structures of the basal nuclei
- Explain the arrangement of gray and white matter in the spinal cord

The brain and the spinal cord are the central nervous system, and they represent the main organs of the nervous system. The spinal cord is a single structure, whereas the adult brain is described in terms of four major regions: the cerebrum, the diencephalon, the brain stem, and the cerebellum. A person's conscious experiences are based on neural activity in the brain. The regulation of homeostasis is governed by a specialized region in the brain. The coordination of reflexes depends on the integration of sensory and motor pathways in the spinal cord.

The Cerebrum

The iconic gray mantle of the human brain, which appears to make up most of the mass of the brain, is the **cerebrum** (Figure 13.6). The wrinkled portion is the **cerebral cortex**, and the rest of the structure is beneath that outer covering. There is a large separation between the two sides of the cerebrum called the **longitudinal fissure**. It separates the cerebrum into two distinct halves, a right and left **cerebral hemisphere**. Deep within the cerebrum, the white matter of the **corpus callosum** provides the major pathway for communication between the two hemispheres of the cerebral cortex.

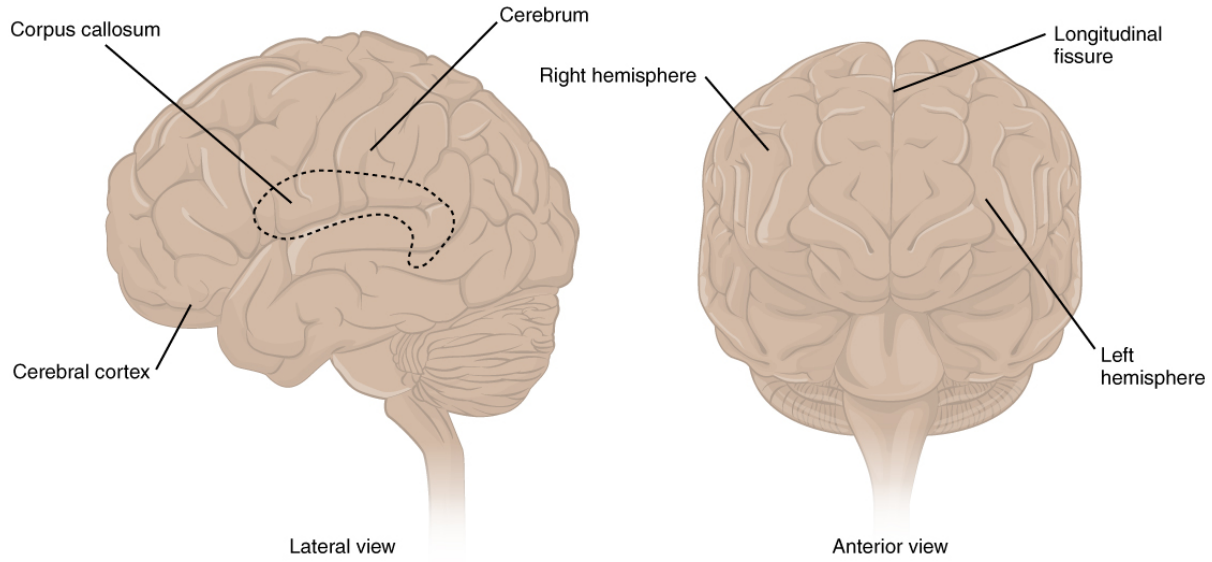


FIGURE 13.6 The Cerebrum The cerebrum is a large component of the CNS in humans, and the most obvious aspect of it is the folded surface called the cerebral cortex.

Many of the higher neurological functions, such as memory, emotion, and consciousness, are the result of cerebral function. The complexity of the cerebrum is different across vertebrate species. The cerebrum of the most primitive vertebrates is not much more than the connection for the sense of smell. In mammals, the cerebrum comprises the outer gray matter that is the cortex (from the Latin word meaning "bark of a tree") and several deep nuclei that belong to three important functional groups. The **basal nuclei** are responsible for cognitive processing, the most important function being that associated with planning movements. The **basal forebrain** contains nuclei that are important in learning and memory. The **limbic cortex** is the region of the cerebral cortex that is part of the **limbic system**, a collection of structures involved in emotion, memory, and behavior.

Cerebral Cortex

The cerebrum is covered by a continuous layer of gray matter that wraps around either side of the forebrain—the cerebral cortex. This thin, extensive region of wrinkled gray matter is responsible for the higher functions of the nervous system. A **gyrus** (plural = gyri) is the ridge of one of those wrinkles, and a **sulcus** (plural = sulci) is the groove between two gyri. The pattern of these folds of tissue indicates specific regions of the cerebral cortex.

The head is limited by the size of the birth canal, and the brain must fit inside the cranial cavity of the skull. Extensive folding in the cerebral cortex enables more gray matter to fit into this limited space. If the gray matter of the cortex were peeled off of the cerebrum and laid out flat, its surface area would be roughly equal to one square meter.

The folding of the cortex maximizes the amount of gray matter in the cranial cavity. During embryonic development, as the telencephalon expands within the skull, the brain goes through a regular course of growth that results in everyone's brain having a similar pattern of folds. The surface of the brain can be mapped on the basis of the locations of large gyri and sulci. Using these landmarks, the cortex can be separated into four major regions, or lobes (Figure 13.7). The **lateral sulcus** that separates the **temporal lobe** from the other regions is one such landmark. Superior to the lateral sulcus are the **parietal lobe** and **frontal lobe**, which are separated from each other by the **central sulcus**. The posterior region of the cortex is the **occipital lobe**, which has no obvious anatomical border between it and the parietal or temporal lobes on the lateral surface of the brain. From the medial surface, an

obvious landmark separating the parietal and occipital lobes is called the **parieto-occipital sulcus**. The fact that there is no obvious anatomical border between these lobes is consistent with the functions of these regions being interrelated.

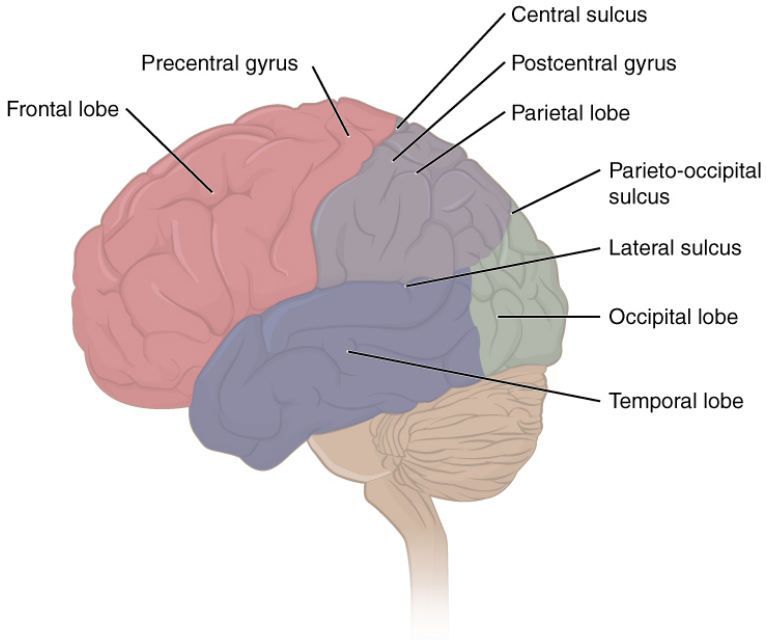


FIGURE 13.7 Lobes of the Cerebral Cortex The cerebral cortex is divided into four lobes. Extensive folding increases the surface area available for cerebral functions.

Different regions of the cerebral cortex can be associated with particular functions, a concept known as localization of function. In the early 1900s, a German neuroscientist named Korbinian Brodmann performed an extensive study of the microscopic anatomy—the cytoarchitecture—of the cerebral cortex and divided the cortex into 52 separate regions on the basis of the histology of the cortex. His work resulted in a system of classification known as **Brodmann's areas**, which is still used today to describe the anatomical distinctions within the cortex (Figure 13.8). The results from Brodmann's work on the anatomy align very well with the functional differences within the cortex. Areas 17 and 18 in the occipital lobe are responsible for primary visual perception. That visual information is complex, so it is processed in the temporal and parietal lobes as well.

The temporal lobe is associated with primary auditory sensation, known as Brodmann's areas 41 and 42 in the superior temporal lobe. Because regions of the temporal lobe are part of the limbic system, memory is an important function associated with that lobe. Memory is essentially a sensory function; memories are recalled sensations such as the smell of Mom's baking or the sound of a barking dog. Even memories of movement are really the memory of sensory feedback from those movements, such as stretching muscles or the movement of the skin around a joint. Structures in the temporal lobe are responsible for establishing long-term memory, but the ultimate location of those memories is usually in the region in which the sensory perception was processed.

The main sensation associated with the parietal lobe is **somatosensation**, meaning the general sensations associated with the body. Posterior to the central sulcus is the **postcentral gyrus**, the primary somatosensory cortex, which is identified as Brodmann's areas 1, 2, and 3. All of the tactile senses are processed in this area, including touch, pressure, tickle, pain, itch, and vibration, as well as more general senses of the body such as **proprioception** and **kinesthesia**, which are the senses of body position and movement, respectively.

Anterior to the central sulcus is the frontal lobe, which is primarily associated with motor functions. The **precentral gyrus** is the primary motor cortex. Cells from this region of the cerebral cortex are the upper motor neurons that instruct cells in the spinal cord to move skeletal muscles. Anterior to this region are a few areas that are associated with planned movements. The **premotor area** is responsible for thinking of a movement to be made. The **frontal eye fields** are important in eliciting eye movements and in attending to visual stimuli. **Broca's area** is responsible for the production of language, or controlling movements responsible for speech; in the vast majority of people, it is located only on the left side. Anterior to these regions is the **prefrontal lobe**, which serves cognitive functions that can be

the basis of personality, short-term memory, and consciousness. The prefrontal lobotomy is an outdated mode of treatment for personality disorders (psychiatric conditions) that profoundly affected the personality of the patient.

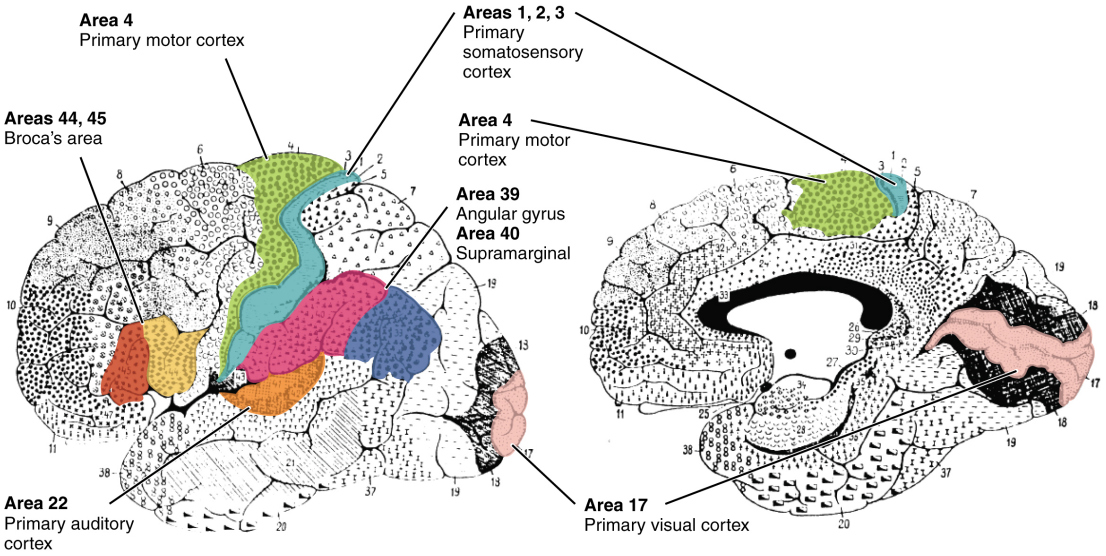


FIGURE 13.8 Brodmann's Areas of the Cerebral Cortex Brodmann mapping of functionally distinct regions of the cortex was based on its cytoarchitecture at a microscopic level.

Subcortical structures

Beneath the cerebral cortex are sets of nuclei known as **subcortical nuclei** that augment cortical processes. The nuclei of the basal forebrain serve as the primary location for acetylcholine production, which modulates the overall activity of the cortex, possibly leading to greater attention to sensory stimuli. Alzheimer's disease is associated with a loss of neurons in the basal forebrain. The **hippocampus** and **amygdala** are medial-lobe structures that, along with the adjacent cortex, are involved in long-term memory formation and emotional responses. The basal nuclei are a set of nuclei in the cerebrum responsible for comparing cortical processing with the general state of activity in the nervous system to influence the likelihood of movement taking place. For example, while a student is sitting in a classroom listening to a lecture, the basal nuclei will keep the urge to jump up and scream from actually happening. (The basal nuclei are also referred to as the basal ganglia, although that is potentially confusing because the term ganglia is typically used for peripheral structures.)

The major structures of the basal nuclei that control movement are the **caudate**, **putamen**, and **globus pallidus**, which are located deep in the cerebrum. The caudate is a long nucleus that follows the basic C-shape of the cerebrum from the frontal lobe, through the parietal and occipital lobes, into the temporal lobe. The putamen is mostly deep in the anterior regions of the frontal and parietal lobes. Together, the caudate and putamen are called the **striatum**. The globus pallidus is a layered nucleus that lies just medial to the putamen; they are called the lenticular nuclei because they look like curved pieces fitting together like lenses. The globus pallidus has two subdivisions, the external and internal segments, which are lateral and medial, respectively. These nuclei are depicted in a frontal section of the brain in Figure 13.9.

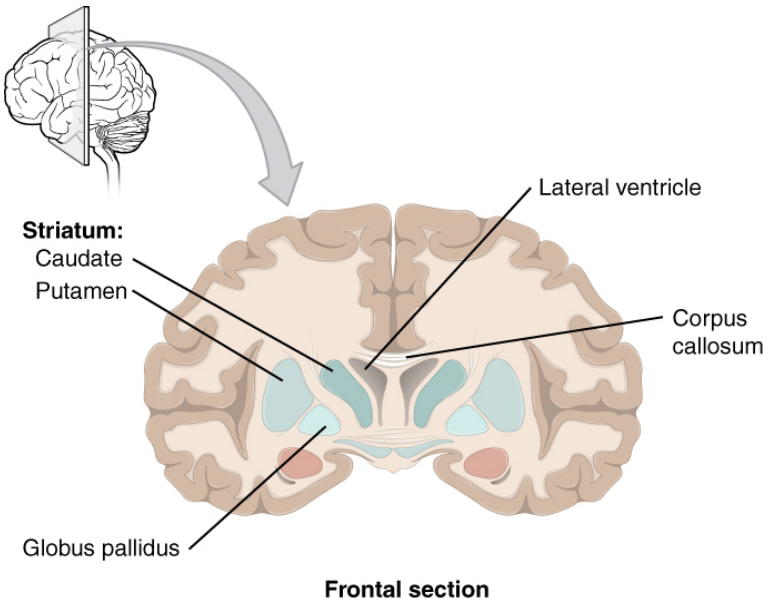


FIGURE 13.9 Frontal Section of Cerebral Cortex and Basal Nuclei The major components of the basal nuclei, shown in a frontal section of the brain, are the caudate (just lateral to the lateral ventricle), the putamen (inferior to the caudate and separated by the large white-matter structure called the internal capsule), and the globus pallidus (medial to the putamen).

The basal nuclei in the cerebrum are connected with a few more nuclei in the brain stem that together act as a functional group that forms a motor pathway. Two streams of information processing take place in the basal nuclei. All input to the basal nuclei is from the cortex into the striatum (Figure 13.10). The **direct pathway** is the projection of axons from the striatum to the globus pallidus internal segment (GPi) and the **substantia nigra pars reticulata** (SNr). The GPi/SNr then projects to the thalamus, which projects back to the cortex. The **indirect pathway** is the projection of axons from the striatum to the globus pallidus external segment (GPe), then to the subthalamic nucleus (STN), and finally to GPi/SNr. The two streams both target the GPi/SNr, but one has a direct projection and the other goes through a few intervening nuclei. The direct pathway causes the **disinhibition** of the thalamus (inhibition of one cell on a target cell that then inhibits the first cell), whereas the indirect pathway causes, or reinforces, the normal inhibition of the thalamus. The thalamus then can either excite the cortex (as a result of the direct pathway) or fail to excite the cortex (as a result of the indirect pathway).

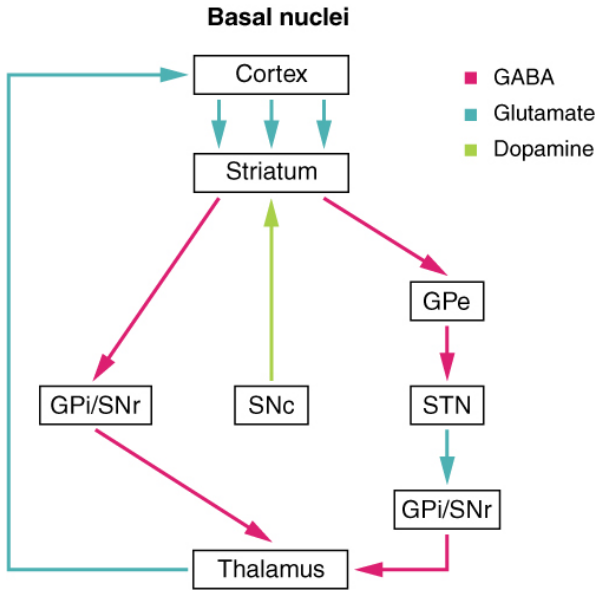


FIGURE 13.10 Connections of Basal Nuclei Input to the basal nuclei is from the cerebral cortex, which is an excitatory connection releasing glutamate as a neurotransmitter. This input is to the striatum, or the caudate and putamen. In the direct pathway, the striatum projects to the internal segment of the globus pallidus and the substantia nigra pars reticulata (GPi/SNr). This is an inhibitory pathway, in which GABA is released at the synapse, and the target cells are hyperpolarized and less likely to fire. The output from the basal nuclei is to the thalamus, which is an inhibitory projection using GABA. The diagram also includes the substantia nigra compacta (SNc), globus pallidus

external segment (GPe), and subthalamic nucleus (STN).

The switch between the two pathways is the **substantia nigra pars compacta**, which projects to the striatum and releases the neurotransmitter dopamine. Dopamine receptors are either excitatory (D1-type receptors) or inhibitory (D2-type receptors). The direct pathway is activated by dopamine, and the indirect pathway is inhibited by dopamine. When the substantia nigra pars compacta is firing, it signals to the basal nuclei that the body is in an active state, and movement will be more likely. When the substantia nigra pars compacta is silent, the body is in a passive state, and movement is inhibited. To illustrate this situation, while a student is sitting listening to a lecture, the substantia nigra pars compacta would be silent and the student less likely to get up and walk around. Likewise, while the professor is lecturing, and walking around at the front of the classroom, the professor's substantia nigra pars compacta would be active, in keeping with their activity level.

INTERACTIVE LINK

Watch this video (http://openstax.org/l/basalnuclei1) to learn about the basal nuclei (also known as the basal ganglia), which have two pathways that process information within the cerebrum. As shown in this video, the direct pathway is the shorter pathway through the system that results in increased activity in the cerebral cortex and increased motor activity. The direct pathway is described as resulting in "disinhibition" of the thalamus. What does disinhibition mean? What are the two neurons doing individually to cause this?

INTERACTIVE LINK

Watch this video (http://openstax.org/l/basalnuclei2) to learn about the basal nuclei (also known as the basal ganglia), which have two pathways that process information within the cerebrum. As shown in this video, the indirect pathway is the longer pathway through the system that results in decreased activity in the cerebral cortex, and therefore less motor activity. The indirect pathway has an extra couple of connections in it, including disinhibition of the subthalamic nucleus. What is the end result on the thalamus, and therefore on movement initiated by the cerebral cortex?

Everyday Connection

The Myth of Left Brain/Right Brain

There is a persistent myth that people are "right-brained" or "left-brained," which is an oversimplification of an important concept about the cerebral hemispheres. There is some lateralization of function, in which the left side of the brain is devoted to language function and the right side is devoted to spatial and nonverbal reasoning. Whereas these functions are predominantly associated with those sides of the brain, there is no monopoly by either side on these functions. Many pervasive functions, such as language, are distributed globally around the cerebrum.

Some of the support for this misconception has come from studies of split brains. A drastic way to deal with a rare and devastating neurological condition (intractable epilepsy) is to separate the two hemispheres of the brain. After sectioning the corpus callosum, a split-brained patient will have trouble producing verbal responses on the basis of sensory information processed on the right side of the cerebrum, leading to the idea that the left side is responsible for language function.

However, there are well-documented cases of language functions lost from damage to the right side of the brain. The deficits seen in damage to the left side of the brain are classified as aphasia, a loss of speech function; damage on the right side can affect the use of language. Right-side damage can result in a loss of ability to understand figurative aspects of speech, such as jokes, irony, or metaphors. Nonverbal aspects of speech can be affected by damage to the right side, such as facial expression or body language, and right-side damage can lead to a "flat affect" in speech, or a loss of emotional expression in speech—sounding like a robot when talking.

The Diencephalon

The diencephalon is the one region of the adult brain that retains its name from embryologic development. The etymology of the word diencephalon translates to "through brain." It is the connection between the cerebrum and

the rest of the nervous system, with one exception. The rest of the brain, the spinal cord, and the PNS all send information to the cerebrum through the diencephalon. Output from the cerebrum passes through the diencephalon. The single exception is the system associated with **olfaction**, or the sense of smell, which connects directly with the cerebrum. In the earliest vertebrate species, the cerebrum was not much more than olfactory bulbs that received peripheral information about the chemical environment (to call it smell in these organisms is imprecise because they lived in the ocean).

The diencephalon is deep beneath the cerebrum and constitutes the walls of the third ventricle. The diencephalon can be described as any region of the brain with "thalamus" in its name. The two major regions of the diencephalon are the thalamus itself and the hypothalamus (Figure 13.11). There are other structures, such as the **epithalamus**, which contains the pineal gland, or the **subthalamus**, which includes the subthalamic nucleus that is part of the basal nuclei.

Thalamus

The **thalamus** is a collection of nuclei that relay information between the cerebral cortex and the periphery, spinal cord, or brain stem. All sensory information, except for the sense of smell, passes through the thalamus before processing by the cortex. Axons from the peripheral sensory organs, or intermediate nuclei, synapse in the thalamus, and thalamic neurons project directly to the cerebrum. It is a requisite synapse in any sensory pathway, except for olfaction. The thalamus does not just pass the information on, it also processes that information. For example, the portion of the thalamus that receives visual information will influence what visual stimuli are important, or what receives attention.

The cerebrum also sends information down to the thalamus, which usually communicates motor commands. This involves interactions with the cerebellum and other nuclei in the brain stem. The cerebrum interacts with the basal nuclei, which involves connections with the thalamus. The primary output of the basal nuclei is to the thalamus, which relays that output to the cerebral cortex. The cortex also sends information to the thalamus that will then influence the effects of the basal nuclei.

Hypothalamus

Inferior and slightly anterior to the thalamus is the **hypothalamus**, the other major region of the diencephalon. The hypothalamus is a collection of nuclei that are largely involved in regulating homeostasis. The hypothalamus is the executive region in charge of the autonomic nervous system and the endocrine system through its regulation of the anterior pituitary gland. Other parts of the hypothalamus are involved in memory and emotion as part of the limbic system.

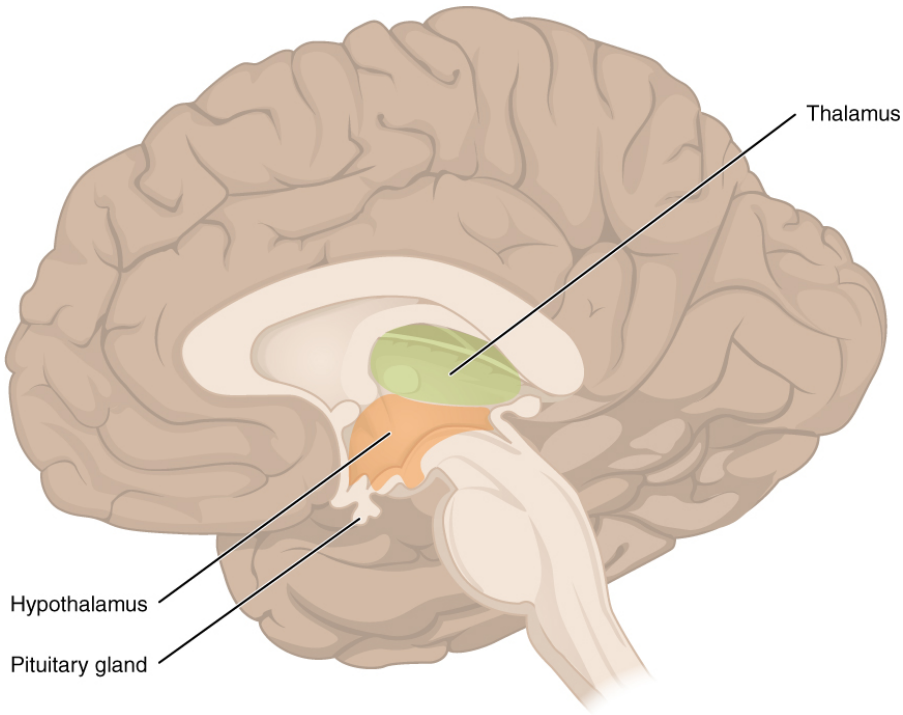


FIGURE 13.11 The Diencephalon The diencephalon is composed primarily of the thalamus and hypothalamus, which together define the walls of the third ventricle. The thalami are two elongated, ovoid structures on either side of the midline that make contact in the middle. The hypothalamus is inferior and anterior to the thalamus, culminating in a sharp angle to which the pituitary gland is attached.

Brain Stem

The midbrain and hindbrain (composed of the pons and the medulla) are collectively referred to as the brain stem (Figure 13.12). The structure emerges from the ventral surface of the forebrain as a tapering cone that connects the brain to the spinal cord. Attached to the brain stem, but considered a separate region of the adult brain, is the cerebellum. The midbrain coordinates sensory representations of the visual, auditory, and somatosensory perceptual spaces. The pons is the main connection with the cerebellum. The pons and the medulla regulate several crucial functions, including the cardiovascular and respiratory systems and rates.

The cranial nerves connect through the brain stem and provide the brain with the sensory input and motor output associated with the head and neck, including most of the special senses. The major ascending and descending pathways between the spinal cord and brain, specifically the cerebrum, pass through the brain stem.

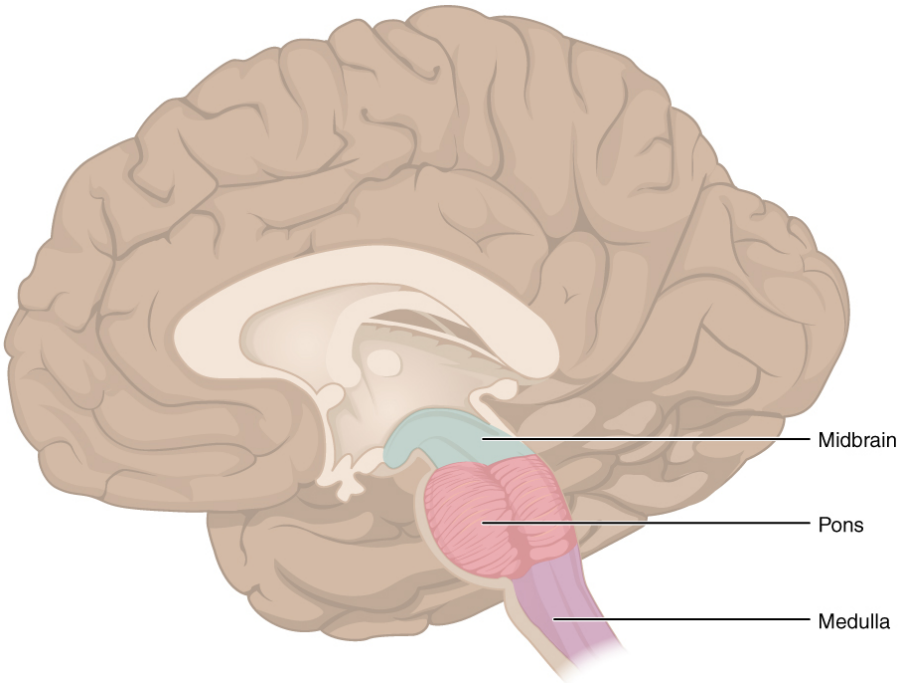


FIGURE 13.12 The Brain Stem The brain stem comprises three regions: the midbrain, the pons, and the medulla.

Midbrain

One of the original regions of the embryonic brain, the midbrain is a small region between the thalamus and pons. It is separated into the **tectum** and **tegmentum**, from the Latin words for roof and floor, respectively. The cerebral aqueduct passes through the center of the midbrain, such that these regions are the roof and floor of that canal.

The tectum is composed of four bumps known as the colliculi (singular = colliculus), which means "little hill" in Latin. The **inferior colliculus** is the inferior pair of these enlargements and is part of the auditory brain stem pathway. Neurons of the inferior colliculus project to the thalamus, which then sends auditory information to the cerebrum for the conscious perception of sound. The **superior colliculus** is the superior pair and combines sensory information about visual space, auditory space, and somatosensory space. Activity in the superior colliculus is related to orienting the eyes to a sound or touch stimulus. If you are walking along the sidewalk on campus and you hear chirping, the superior colliculus coordinates that information with your awareness of the visual location of the tree right above you. That is the correlation of auditory and visual maps. If you suddenly feel something wet fall on your head, your superior colliculus integrates that with the auditory and visual maps and you know that the chirping bird just relieved itself on you. You want to look up to see the culprit, but do not.

The tegmentum is continuous with the gray matter of the rest of the brain stem. Throughout the midbrain, pons, and medulla, the tegmentum contains the nuclei that receive and send information through the cranial nerves, as well as regions that regulate important functions such as those of the cardiovascular and respiratory systems.

Pons

The word pons comes from the Latin word for bridge. It is visible on the anterior surface of the brain stem as the thick bundle of white matter attached to the cerebellum. The pons is the main connection between the cerebellum and the brain stem. The bridge-like white matter is only the anterior surface of the pons; the gray matter beneath that is a continuation of the tegmentum from the midbrain. Gray matter in the tegmentum region of the pons contains neurons receiving descending input from the forebrain that is sent to the cerebellum.

Medulla

The medulla is the region known as the myelencephalon in the embryonic brain. The initial portion of the name, "myel," refers to the significant white matter found in this region—especially on its exterior, which is continuous with the white matter of the spinal cord. The tegmentum of the midbrain and pons continues into the medulla because this gray matter is responsible for processing cranial nerve information. A diffuse region of gray matter throughout the brain stem, known as the **reticular formation**, is related to sleep and wakefulness, such as general brain activity

and attention.

The Cerebellum

The **cerebellum**, as the name suggests, is the "little brain." It is covered in gyri and sulci like the cerebrum, and looks like a miniature version of that part of the brain (Figure 13.13). The cerebellum is largely responsible for comparing information from the cerebrum with sensory feedback from the periphery through the spinal cord. It accounts for approximately 10 percent of the mass of the brain.

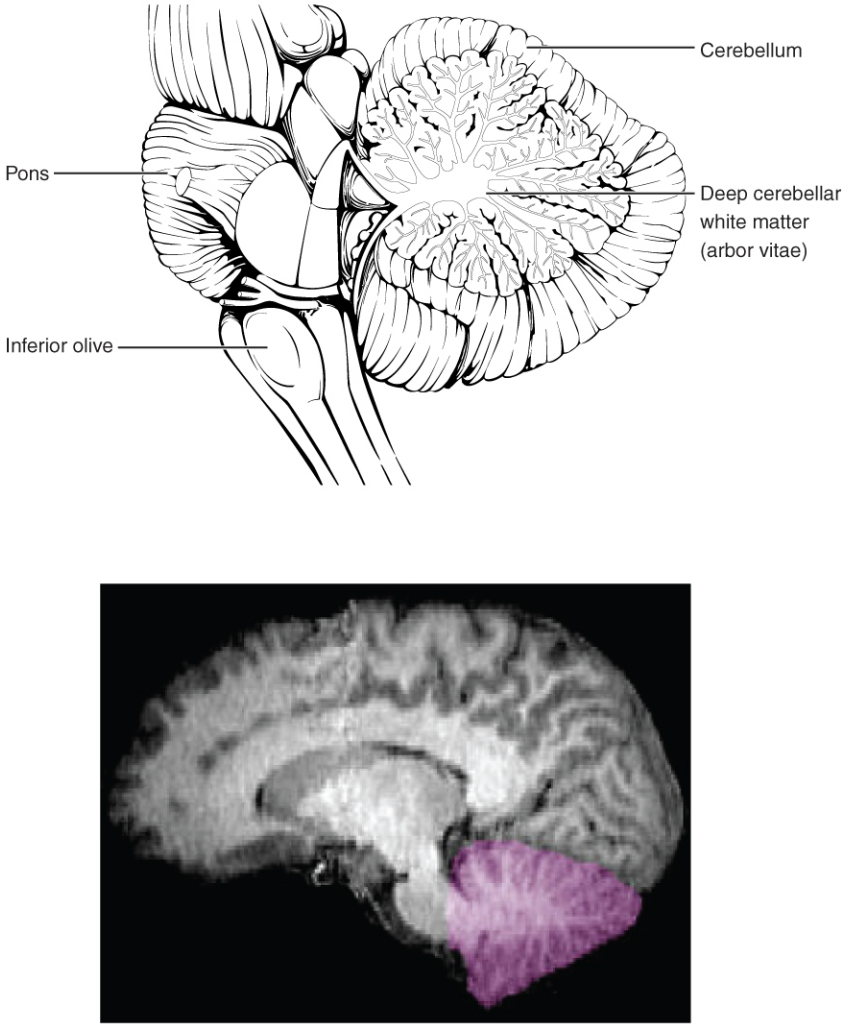


FIGURE 13.13 The Cerebellum The cerebellum is situated on the posterior surface of the brain stem. Descending input from the cerebellum enters through the large white matter structure of the pons. Ascending input from the periphery and spinal cord enters through the fibers of the inferior olive. Output goes to the midbrain, which sends a descending signal to the spinal cord.

Descending fibers from the cerebrum have branches that connect to neurons in the pons. Those neurons project into the cerebellum, providing a copy of motor commands sent to the spinal cord. Sensory information from the periphery, which enters through spinal or cranial nerves, is copied to a nucleus in the medulla known as the **inferior olive**. Fibers from this nucleus enter the cerebellum and are compared with the descending commands from the cerebrum. If the primary motor cortex of the frontal lobe sends a command down to the spinal cord to initiate walking, a copy of that instruction is sent to the cerebellum. Sensory feedback from the muscles and joints, proprioceptive information about the movements of walking, and sensations of balance are sent to the cerebellum through the inferior olive and the cerebellum compares them. If walking is not coordinated, perhaps because the ground is uneven or a strong wind is blowing, then the cerebellum sends out a corrective command to compensate for the difference between the original cortical command and the sensory feedback. The output of the cerebellum is into the midbrain, which then sends a descending input to the spinal cord to correct the messages going to skeletal muscles.

The Spinal Cord

The description of the CNS is concentrated on the structures of the brain, but the spinal cord is another major organ of the system. Whereas the brain develops out of expansions of the neural tube into primary and then secondary vesicles, the spinal cord maintains the tube structure and is only specialized into certain regions. As the spinal cord continues to develop in the newborn, anatomical features mark its surface. The anterior midline is marked by the **anterior median fissure**, and the posterior midline is marked by the **posterior median sulcus**. Axons enter the posterior side through the **dorsal (posterior) nerve root**, which marks the **posterolateral sulcus** on either side. The axons emerging from the anterior side do so through the **ventral (anterior) nerve root**. Note that it is common to see the terms dorsal (dorsal = "back") and ventral (ventral = "belly") used interchangeably with posterior and anterior, particularly in reference to nerves and the structures of the spinal cord. You should learn to be comfortable with both.

On the whole, the posterior regions are responsible for sensory functions and the anterior regions are associated with motor functions. This comes from the initial development of the spinal cord, which is divided into the **basal plate** and the **alar plate**. The basal plate is closest to the ventral midline of the neural tube, which will become the anterior face of the spinal cord and gives rise to motor neurons. The alar plate is on the dorsal side of the neural tube and gives rise to neurons that will receive sensory input from the periphery.

The length of the spinal cord is divided into regions that correspond to the regions of the vertebral column. The name of a spinal cord region corresponds to the level at which spinal nerves pass through the intervertebral foramina. Immediately adjacent to the brain stem is the cervical region, followed by the thoracic, then the lumbar, and finally the sacral region. The spinal cord is not the full length of the vertebral column because the spinal cord does not grow significantly longer after the first or second year, but the skeleton continues to grow. The nerves that emerge from the spinal cord pass through the intervertebral foramina at the respective levels. As the vertebral column grows, these nerves grow with it and result in a long bundle of nerves that resembles a horse's tail and is named the **cauda equina**. The sacral spinal cord is at the level of the upper lumbar vertebral bones. The spinal nerves extend from their various levels to the proper level of the vertebral column.

Gray Horns

In cross-section, the gray matter of the spinal cord has the appearance of an ink-blot test, with the spread of the gray matter on one side replicated on the other—a shape reminiscent of a bulbous capital "H." As shown in Figure 13.14, the gray matter is subdivided into regions that are referred to as horns. The **posterior horn** is responsible for sensory processing. The **anterior horn** sends out motor signals to the skeletal muscles. The **lateral horn**, which is only found in the thoracic, upper lumbar, and sacral regions, contains cell bodies of motor neurons of the autonomic nervous system.

Some of the largest neurons of the spinal cord are the multipolar motor neurons in the anterior horn. The fibers that cause contraction of skeletal muscles are the axons of these neurons. The motor neuron that causes contraction of the big toe, for example, is located in the sacral spinal cord. The axon that has to reach all the way to the belly of that muscle may be a meter in length. The neuronal cell body that maintains that long fiber must be quite large, possibly several hundred micrometers in diameter, making it one of the largest cells in the body.

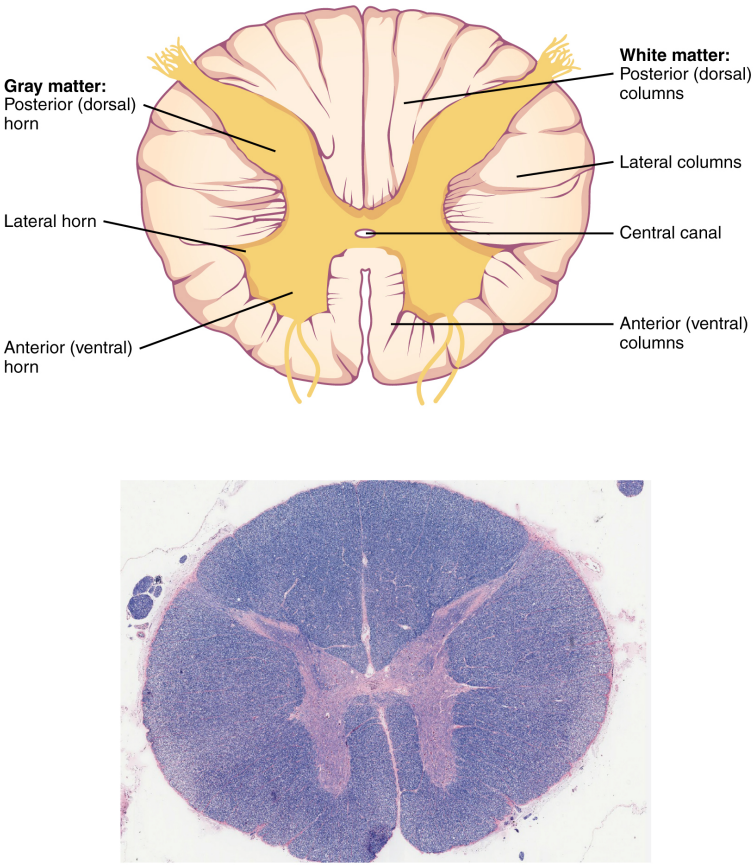


FIGURE 13.14 Cross-section of Spinal Cord The cross-section of a thoracic spinal cord segment shows the posterior, anterior, and lateral horns of gray matter, as well as the posterior, anterior, and lateral columns of white matter. LM × 40. (Micrograph provided by the Regents of University of Michigan Medical School © 2012)

White Columns

Just as the gray matter is separated into horns, the white matter of the spinal cord is separated into columns. **Ascending tracts** of nervous system fibers in these columns carry sensory information up to the brain, whereas **descending tracts** carry motor commands from the brain. Looking at the spinal cord longitudinally, the columns extend along its length as continuous bands of white matter. Between the two posterior horns of gray matter are the **posterior columns**. Between the two anterior horns, and bounded by the axons of motor neurons emerging from that gray matter area, are the **anterior columns**. The white matter on either side of the spinal cord, between the posterior horn and the axons of the anterior horn neurons, are the **lateral columns**. The posterior columns are composed of axons of ascending tracts. The anterior and lateral columns are composed of many different groups of axons of both ascending and descending tracts—the latter carrying motor commands down from the brain to the spinal cord to control output to the periphery.

INTERACTIVE LINK

Watch this video (http://openstax.org/l/graymatter) to learn about the gray matter of the spinal cord that receives input from fibers of the dorsal (posterior) root and sends information out through the fibers of the ventral (anterior) root. As discussed in this video, these connections represent the interactions of the CNS with peripheral structures for both sensory and motor functions. The cervical and lumbar spinal cords have enlargements as a result of larger populations of neurons. What are these enlargements responsible for?

Disorders of the...

Basal Nuclei

Parkinson's disease is a disorder of the basal nuclei, specifically of the substantia nigra, that demonstrates the

effects of the direct and indirect pathways. Parkinson's disease is the result of neurons in the substantia nigra pars compacta dying. These neurons release dopamine into the striatum. Without that modulatory influence, the basal nuclei are stuck in the indirect pathway, without the direct pathway being activated. The direct pathway is responsible for increasing cortical movement commands. The increased activity of the indirect pathway results in the hypokinetic disorder of Parkinson's disease.

Parkinson's disease is neurodegenerative, meaning that neurons die that cannot be replaced, so there is no cure for the disorder. Treatments for Parkinson's disease are aimed at increasing dopamine levels in the striatum. Currently, the most common way of doing that is by providing the amino acid L-DOPA, which is a precursor to the neurotransmitter dopamine and can cross the blood-brain barrier. With levels of the precursor elevated, the remaining cells of the substantia nigra pars compacta can make more neurotransmitter and have a greater effect. Unfortunately, the patient will become less responsive to L-DOPA treatment as time progresses, and it can cause increased dopamine levels elsewhere in the brain, which are associated with psychosis or schizophrenia.

INTERACTIVE LINK

Visit this site (http://openstax.org/l/parkinsons) for a thorough explanation of Parkinson's disease.

INTERACTIVE LINK

Compared with the nearest evolutionary relative, the chimpanzee, the human has a brain that is huge. At a point in the past, a common ancestor gave rise to the two species of humans and chimpanzees. That evolutionary history is long and is still an area of intense study. But something happened to increase the size of the human brain relative to the chimpanzee. Read this article (http://openstax.org/l/hugebrain) in which the author explores the current understanding of why this happened.

According to one hypothesis about the expansion of brain size, what tissue might have been sacrificed so energy was available to grow our larger brain? Based on what you know about that tissue and nervous tissue, why would there be a trade-off between them in terms of energy use?

13.3 Circulation and the Central Nervous System

LEARNING OBJECTIVES

By the end of this section, you will be able to:

- Describe the vessels that supply the CNS with blood
- Name the components of the ventricular system and the regions of the brain in which each is located
- Explain the production of cerebrospinal fluid and its flow through the ventricles
- Explain how a disruption in circulation would result in a stroke

The CNS is crucial to the operation of the body, and any compromise in the brain and spinal cord can lead to severe difficulties. The CNS has a privileged blood supply, as suggested by the blood-brain barrier. The function of the tissue in the CNS is crucial to the survival of the organism, so the contents of the blood cannot simply pass into the central nervous tissue. To protect this region from the toxins and pathogens that may be traveling through the blood stream, there is strict control over what can move out of the general systems and into the brain and spinal cord. Because of this privilege, the CNS needs specialized structures for the maintenance of circulation. This begins with a unique arrangement of blood vessels carrying fresh blood into the CNS. Beyond the supply of blood, the CNS filters that blood into cerebrospinal fluid (CSF), which is then circulated through the cavities of the brain and spinal cord called ventricles.

Blood Supply to the Brain

A lack of oxygen to the CNS can be devastating, and the cardiovascular system has specific regulatory reflexes to ensure that the blood supply is not interrupted. There are multiple routes for blood to get into the CNS, with specializations to protect that blood supply and to maximize the ability of the brain to get an uninterrupted perfusion.

Arterial Supply

The major artery carrying recently oxygenated blood away from the heart is the aorta. The very first branches off the aorta supply the heart with nutrients and oxygen. The next branches give rise to the **common carotid arteries**, which further branch into the **internal carotid arteries**. The external carotid arteries supply blood to the tissues on the surface of the cranium. The bases of the common carotids contain stretch receptors that immediately respond to the drop in blood pressure upon standing. The **orthostatic reflex** is a reaction to this change in body position, so that blood pressure is maintained against the increasing effect of gravity (orthostatic means "standing up"). Heart rate increases—a reflex of the sympathetic division of the autonomic nervous system—and this raises blood pressure.

The internal carotid artery enters the cranium through the **carotid canal** in the temporal bone. A second set of vessels that supply the CNS are the **vertebral arteries**, which are protected as they pass through the neck region by the transverse foramina of the cervical vertebrae. The vertebral arteries enter the cranium through the **foramen magnum** of the occipital bone. Branches off the left and right vertebral arteries merge into the **anterior spinal artery** supplying the anterior aspect of the spinal cord, found along the anterior median fissure. The two vertebral arteries then merge into the **basilar artery**, which gives rise to branches to the brain stem and cerebellum. The left and right internal carotid arteries and branches of the basilar artery all become the **circle of Willis**, a confluence of arteries that can maintain perfusion of the brain even if narrowing or a blockage limits flow through one part (Figure 13.15).

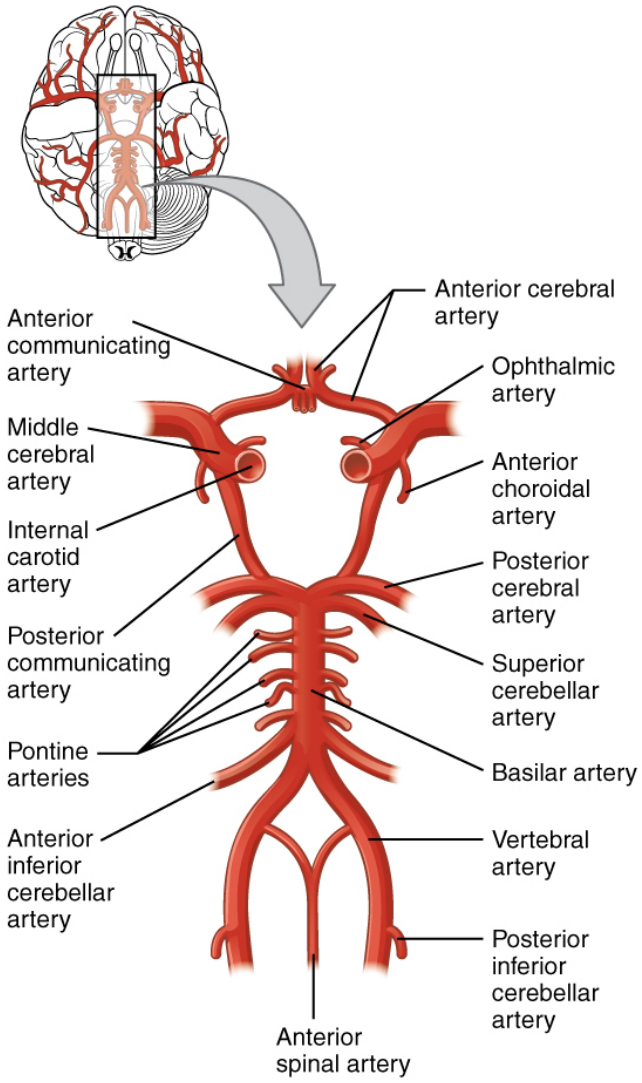


FIGURE 13.15 Circle of Willis The blood supply to the brain enters through the internal carotid arteries and the vertebral arteries, eventually giving rise to the circle of Willis.

INTERACTIVE LINK

Watch this animation (http://openstax.org/l/bloodflow1) to see how blood flows to the brain and passes through the circle of Willis before being distributed through the cerebrum. The circle of Willis is a specialized arrangement of arteries that ensure constant perfusion of the cerebrum even in the event of a blockage of one of the arteries in the circle. The animation shows the normal direction of flow through the circle of Willis to the middle cerebral artery. Where would the blood come from if there were a blockage just posterior to the middle cerebral artery on the left?

Venous Return

After passing through the CNS, blood returns to the circulation through a series of **dural sinuses** and veins (Figure 13.16). The **superior sagittal sinus** runs in the groove of the longitudinal fissure, where it absorbs CSF from the meninges. The superior sagittal sinus drains to the confluence of sinuses, along with the **occipital sinuses** and **straight sinus**, to then drain into the **transverse sinuses**. The transverse sinuses connect to the **sigmoid sinuses**, which then connect to the **jugular veins**. From there, the blood continues toward the heart to be pumped to the lungs for reoxygenation.

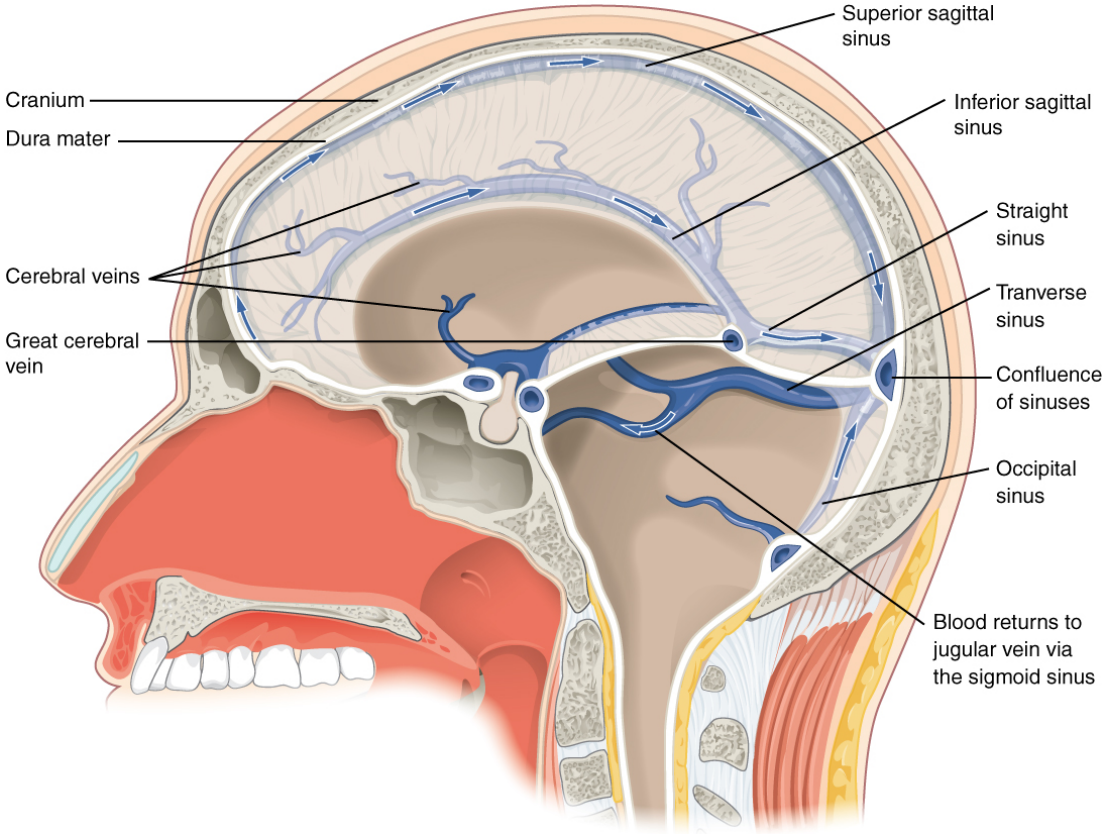


FIGURE 13.16 Dural Sinuses and Veins Blood drains from the brain through a series of sinuses that connect to the jugular veins.

Protective Coverings of the Brain and Spinal Cord

The outer surface of the CNS is covered by a series of membranes composed of connective tissue called the **meninges**, which protect the brain. The **dura mater** is a thick fibrous layer and a strong protective sheath over the entire brain and spinal cord. It is anchored to the inner surface of the cranium and vertebral cavity. The **arachnoid mater** is a membrane of thin fibrous tissue that forms a loose sac around the CNS. Beneath the arachnoid is a thin, filamentous mesh called the **arachnoid trabeculae**, which looks like a spider web, giving this layer its name. Directly adjacent to the surface of the CNS is the **pia mater**, a thin fibrous membrane that follows the convolutions of gyri and sulci in the cerebral cortex and fits into other grooves and indentations (Figure 13.17).

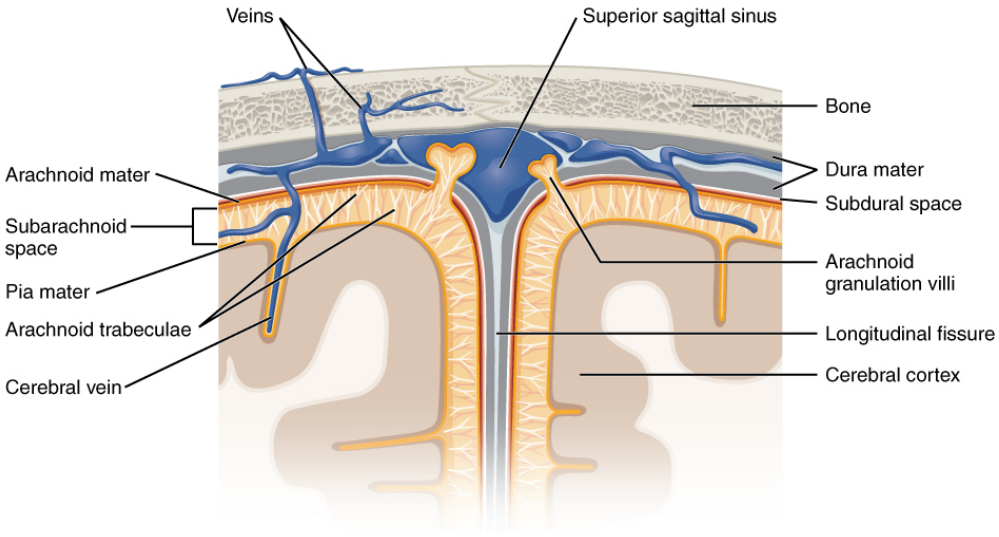


FIGURE 13.17 Meningeal Layers of Superior Sagittal Sinus The layers of the meninges in the longitudinal fissure of the superior sagittal sinus are shown, with the dura mater adjacent to the inner surface of the cranium, the pia mater adjacent to the surface of the brain, and the arachnoid and subarachnoid space between them. An arachnoid villus is shown emerging into the dural sinus to allow CSF to filter back into the blood for drainage.

Dura Mater

Like a thick cap covering the brain, the dura mater is a tough outer covering. The name comes from the Latin for "tough mother" to represent its physically protective role. It encloses the entire CNS and the major blood vessels that enter the cranium and vertebral cavity. It is directly attached to the inner surface of the bones of the cranium and to the very end of the vertebral cavity.

There are infoldings of the dura that fit into large crevasses of the brain. Two infoldings go through the midline separations of the cerebrum and cerebellum; one forms a shelf-like tent between the occipital lobes of the cerebrum and the cerebellum, and the other surrounds the pituitary gland. The dura also surrounds and supports the venous sinuses.

Arachnoid Mater

The middle layer of the meninges is the arachnoid, named for the spider-web–like trabeculae between it and the pia mater. The arachnoid defines a sac-like enclosure around the CNS. The trabeculae are found in the **subarachnoid space**, which is filled with circulating CSF. The arachnoid emerges into the dural sinuses as the **arachnoid granulations**, where the CSF is filtered back into the blood for drainage from the nervous system.

The subarachnoid space is filled with circulating CSF, which also provides a liquid cushion to the brain and spinal cord. Similar to clinical blood work, a sample of CSF can be withdrawn to find chemical evidence of neuropathology or metabolic traces of the biochemical functions of nervous tissue.

Pia Mater

The outer surface of the CNS is covered in the thin fibrous membrane of the pia mater. It is thought to have a continuous layer of cells providing a fluid-impermeable membrane. The name pia mater comes from the Latin for "tender mother," suggesting the thin membrane is a gentle covering for the brain. The pia extends into every convolution of the CNS, lining the inside of the sulci in the cerebral and cerebellar cortices. At the end of the spinal cord, a thin filament extends from the inferior end of CNS at the upper lumbar region of the vertebral column to the sacral end of the vertebral column. Because the spinal cord does not extend through the lower lumbar region of the vertebral column, a needle can be inserted through the dura and arachnoid layers to withdraw CSF. This procedure is called a **lumbar puncture** and avoids the risk of damaging the central tissue of the spinal cord. Blood vessels that are nourishing the central nervous tissue are between the pia mater and the nervous tissue.

Disorders of the...

Meninges

Meningitis is an inflammation of the meninges, the three layers of fibrous membrane that surround the CNS. Meningitis can be caused by infection by bacteria or viruses. The particular pathogens are not special to meningitis; it is just an inflammation of that specific set of tissues from what might be a broader infection. Bacterial meningitis can be caused by *Streptococcus*, *Staphylococcus*, or the tuberculosis pathogen, among many others. Viral meningitis is usually the result of common enteroviruses (such as those that cause intestinal disorders), but may be the result of the herpes virus or West Nile virus. Bacterial meningitis tends to be more severe.

The symptoms associated with meningitis can be fever, chills, nausea, vomiting, light sensitivity, soreness of the neck, or severe headache. More important are the neurological symptoms, such as changes in mental state (confusion, memory deficits, and other dementia-type symptoms). A serious risk of meningitis can be damage to peripheral structures because of the nerves that pass through the meninges. Hearing loss is a common result of meningitis.

The primary test for meningitis is a lumbar puncture. A needle inserted into the lumbar region of the spinal column through the dura mater and arachnoid membrane into the subarachnoid space can be used to withdraw the fluid for chemical testing. Fatality occurs in 5 to 40 percent of children and 20 to 50 percent of adults with bacterial meningitis. Treatment of bacterial meningitis is through antibiotics, but viral meningitis cannot be treated with antibiotics because viruses do not respond to that type of drug. Fortunately, the viral forms are milder.

INTERACTIVE LINK

Watch this video (http://openstax.org/l/lumbarpuncture) that describes the procedure known as the lumbar puncture, a medical procedure used to sample the CSF. Because of the anatomy of the CNS, it is a relative safe location to insert a needle. Why is the lumbar puncture performed in the lower lumbar area of the vertebral column?

The Ventricular System

Cerebrospinal fluid (CSF) circulates throughout and around the CNS. In other tissues, water and small molecules are filtered through capillaries as the major contributor to the interstitial fluid. In the brain, CSF is produced in special structures to perfuse through the nervous tissue of the CNS and is continuous with the interstitial fluid. Specifically, CSF circulates to remove metabolic wastes from the interstitial fluids of nervous tissues and return them to the blood stream. The **ventricles** are the open spaces within the brain where CSF circulates. In some of these spaces, CSF is produced by filtering of the blood that is performed by a specialized membrane known as a choroid plexus. The CSF circulates through all of the ventricles to eventually emerge into the subarachnoid space where it will be reabsorbed into the blood.

The Ventricles

There are four ventricles within the brain, all of which developed from the original hollow space within the neural tube, the **central canal**. The first two are named the **lateral ventricles** and are deep within the cerebrum. These ventricles are connected to the **third ventricle** by two openings called the **interventricular foramina**. The third ventricle is the space between the left and right sides of the diencephalon, which opens into the **cerebral aqueduct** that passes through the midbrain. The aqueduct opens into the **fourth ventricle**, which is the space between the cerebellum and the pons and upper medulla (Figure 13.18).

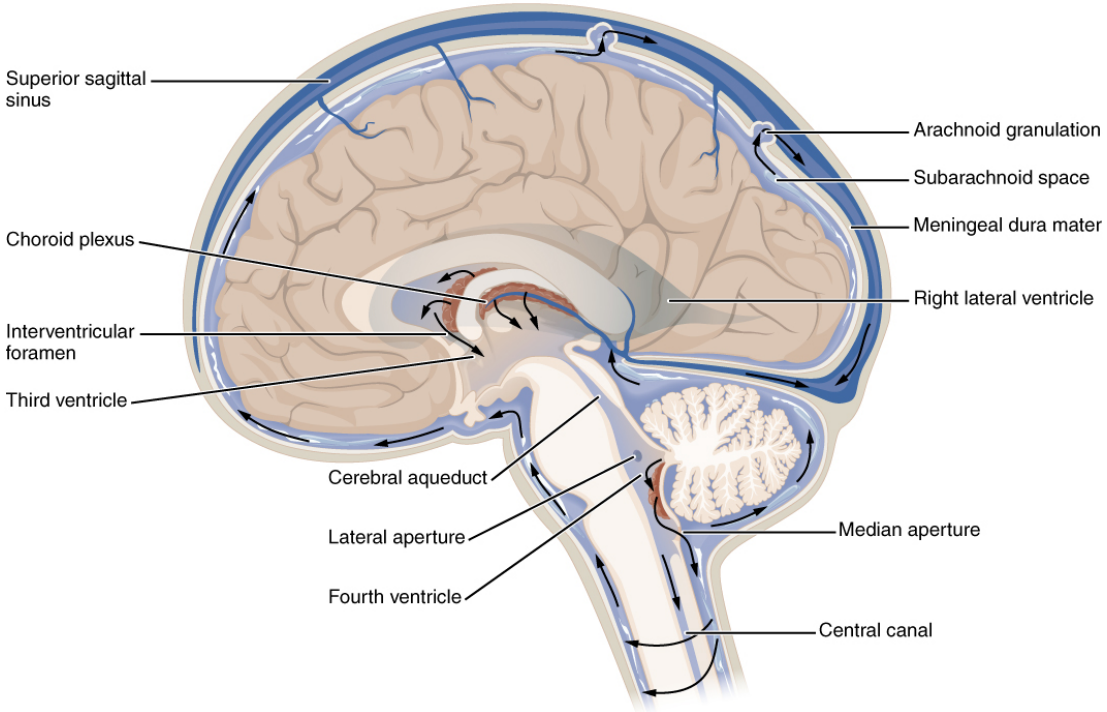


FIGURE 13.18 Cerebrospinal Fluid Circulation The choroid plexus in the four ventricles produce CSF, which is circulated through the ventricular system and then enters the subarachnoid space through the median and lateral apertures. The CSF is then reabsorbed into the blood at the arachnoid granulations, where the arachnoid membrane emerges into the dural sinuses.

As the telencephalon enlarges and grows into the cranial cavity, it is limited by the space within the skull. The telencephalon is the most anterior region of what was the neural tube, but cannot grow past the limit of the frontal bone of the skull. Because the cerebrum fits into this space, it takes on a C-shaped formation, through the frontal, parietal, occipital, and finally temporal regions. The space within the telencephalon is stretched into this same C-shape. The two ventricles are in the left and right sides, and were at one time referred to as the first and second ventricles. The interventricular foramina connect the frontal region of the lateral ventricles with the third ventricle.

The third ventricle is the space bounded by the medial walls of the hypothalamus and thalamus. The two thalami touch in the center in most brains as the massa intermedia, which is surrounded by the third ventricle. The cerebral aqueduct opens just inferior to the epithalamus and passes through the midbrain. The tectum and tegmentum of the midbrain are the roof and floor of the cerebral aqueduct, respectively. The aqueduct opens up into the fourth ventricle. The floor of the fourth ventricle is the dorsal surface of the pons and upper medulla (that gray matter making a continuation of the tegmentum of the midbrain). The fourth ventricle then narrows into the central canal of the spinal cord.

The ventricular system opens up to the subarachnoid space from the fourth ventricle. The single **median aperture** and the pair of **lateral apertures** connect to the subarachnoid space so that CSF can flow through the ventricles and around the outside of the CNS. Cerebrospinal fluid is produced within the ventricles by a type of specialized membrane called a **choroid plexus**. Ependymal cells (one of the types of glial cells described in the introduction to the nervous system) surround blood capillaries and filter the blood to make CSF. The fluid is a clear solution with a limited amount of the constituents of blood. It is essentially water, small molecules, and electrolytes. Oxygen and carbon dioxide are dissolved into the CSF, as they are in blood, and can diffuse between the fluid and the nervous tissue.

Cerebrospinal Fluid Circulation

The choroid plexuses are found in all four ventricles. Observed in dissection, they appear as soft, fuzzy structures that may still be pink, depending on how well the circulatory system is cleared in preparation of the tissue. The CSF is produced from components extracted from the blood, so its flow out of the ventricles is tied to the pulse of cardiovascular circulation.

From the lateral ventricles, the CSF flows into the third ventricle, where more CSF is produced, and then through the

cerebral aqueduct into the fourth ventricle where even more CSF is produced. A very small amount of CSF is filtered at any one of the plexuses, for a total of about 500 milliliters daily, but it is continuously made and pulses through the ventricular system, keeping the fluid moving. From the fourth ventricle, CSF can continue down the central canal of the spinal cord, but this is essentially a cul-de-sac, so more of the fluid leaves the ventricular system and moves into the subarachnoid space through the median and lateral apertures.

Within the subarachnoid space, the CSF flows around all of the CNS, providing two important functions. As with elsewhere in its circulation, the CSF picks up metabolic wastes from the nervous tissue and moves it out of the CNS. It also acts as a liquid cushion for the brain and spinal cord. By surrounding the entire system in the subarachnoid space, it provides a thin buffer around the organs within the strong, protective dura mater. The arachnoid granulations are outpocketings of the arachnoid membrane into the dural sinuses so that CSF can be reabsorbed into the blood, along with the metabolic wastes. From the dural sinuses, blood drains out of the head and neck through the jugular veins, along with the rest of the circulation for blood, to be reoxygenated by the lungs and wastes to be filtered out by the kidneys (Table 13.2).

INTERACTIVE LINK

Watch this animation (http://openstax.org/l/CSFflow) that shows the flow of CSF through the brain and spinal cord, and how it originates from the ventricles and then spreads into the space within the meninges, where the fluids then move into the venous sinuses to return to the cardiovascular circulation. What are the structures that produce CSF and where are they found? How are the structures indicated in this animation?

Components of CSF Circulation

	Lateral ventricles	Third ventricle	Cerebral aqueduct	Fourth ventricle	Central canal	Subarachnoid space
Location in CNS	Cerebrum	Diencephalon	Midbrain	Between pons/upper medulla and cerebellum	Spinal cord	External to entire CNS
Blood vessel structure	Choroid plexus	Choroid plexus	None	Choroid plexus	None	Arachnoid granulations

TABLE 13.2

Disorders of the...

Central Nervous System

The supply of blood to the brain is crucial to its ability to perform many functions. Without a steady supply of oxygen, and to a lesser extent glucose, the nervous tissue in the brain cannot keep up its extensive electrical activity. These nutrients get into the brain through the blood, and if blood flow is interrupted, neurological function is compromised.

The common name for a disruption of blood supply to the brain is a stroke. It is caused by a blockage to an artery in the brain. The blockage is from some type of embolus: a blood clot, a fat embolus, or an air bubble. When the blood cannot travel through the artery, the surrounding tissue that is deprived starves and dies. Strokes will often result in the loss of very specific functions. A stroke in the lateral medulla, for example, can cause a loss in the ability to swallow. Sometimes, seemingly unrelated functions will be lost because they are dependent on structures in the same region. Along with the swallowing in the previous example, a stroke in that region could affect sensory functions from the face or extremities because important white matter pathways also pass through the lateral medulla. Loss of blood flow to specific regions of the cortex can lead to the loss of specific higher functions, from the ability to recognize faces to the ability to move a particular region of the body.

Severe or limited memory loss can be the result of a temporal lobe stroke.

Related to strokes are transient ischemic attacks (TIAs), which can also be called "mini-strokes." These are events in which a physical blockage may be temporary, cutting off the blood supply and oxygen to a region, but not to the extent that it causes cell death in that region. While the neurons in that area are recovering from the event, neurological function may be lost. Function can return if the area is able to recover from the event.

Recovery from a stroke (or TIA) is strongly dependent on the speed of treatment. Often, the person who is present and notices something is wrong must then make a decision. The mnemonic **FAST** helps people remember what to look for when someone is dealing with sudden losses of neurological function. If someone complains of feeling "funny," check these things quickly: Look at the person's face. Do they have problems moving **F**ace muscles and making regular facial expressions? Ask the person to raise their **A**rms above the head. Can the person lift one arm but not the other? Has the person's **S**peech changed? Are they slurring words or having trouble saying things? If any of these things have happened, then it is **T**ime to call for help.

Sometimes, treatment with blood-thinning drugs can alleviate the problem, and recovery is possible. If the tissue is damaged, the amazing thing about the nervous system is that it is adaptable. With physical, occupational, and speech therapy, victims of strokes can recover, or more accurately relearn, functions.

13.4 The Peripheral Nervous System

LEARNING OBJECTIVES

By the end of this section, you will be able to:

- Describe the structures found in the PNS
- Distinguish between somatic and autonomic structures, including the special peripheral structures of the enteric nervous system
- Name the twelve cranial nerves and explain the functions associated with each
- Describe the sensory and motor components of spinal nerves and the plexuses that they pass through

The PNS is not as contained as the CNS because it is defined as everything that is not the CNS. Some peripheral structures are incorporated into the other organs of the body. In describing the anatomy of the PNS, it is necessary to describe the common structures, the nerves and the ganglia, as they are found in various parts of the body. Many of the neural structures that are incorporated into other organs are features of the digestive system; these structures are known as the **enteric nervous system** and are a special subset of the PNS.

Ganglia

A ganglion is a group of neuron cell bodies in the periphery. Ganglia can be categorized, for the most part, as either sensory ganglia or autonomic ganglia, referring to their primary functions. The most common type of sensory ganglion is a **dorsal (posterior) root ganglion**. These ganglia are the cell bodies of neurons with axons that are sensory endings in the periphery, such as in the skin, and that extend into the CNS through the dorsal nerve root. The ganglion is an enlargement of the nerve root. Under microscopic inspection, it can be seen to include the cell bodies of the neurons, as well as bundles of fibers that are the posterior nerve root (Figure 13.19). The cells of the dorsal root ganglion are unipolar cells, classifying them by shape. Also, the small round nuclei of satellite cells can be seen surrounding—as if they were orbiting—the neuron cell bodies.

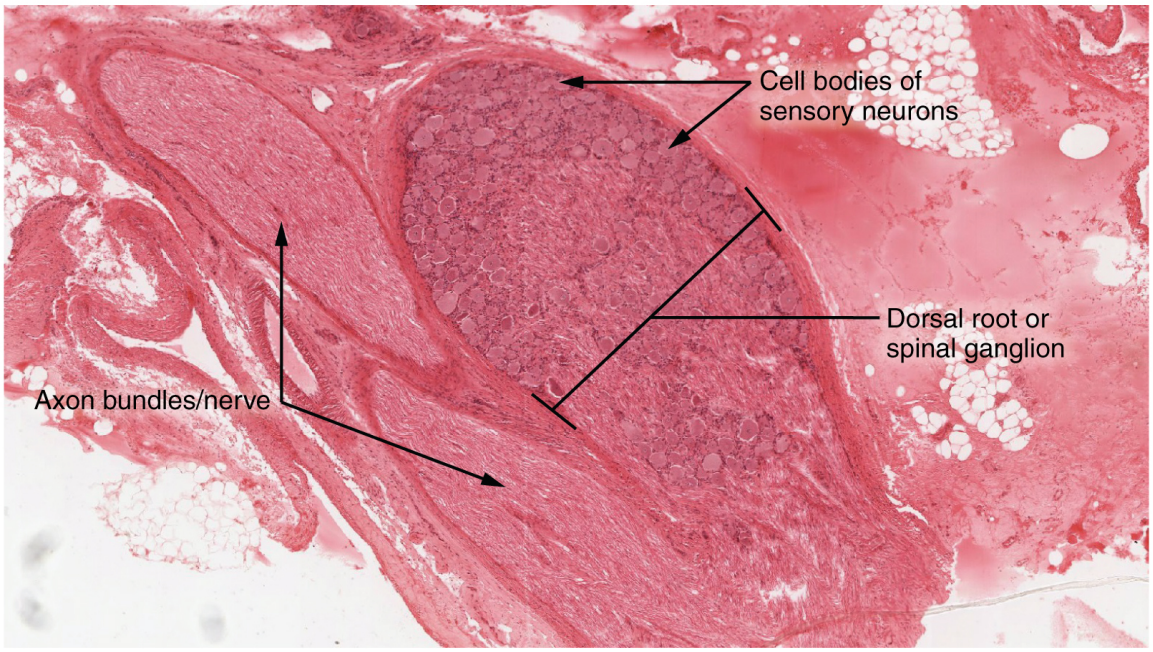


FIGURE 13.19 Dorsal Root Ganglion The cell bodies of sensory neurons, which are unipolar neurons by shape, are seen in this photomicrograph. Also, the fibrous region is composed of the axons of these neurons that are passing through the ganglion to be part of the dorsal nerve root (tissue source: canine). LM × 40. (Micrograph provided by the Regents of University of Michigan Medical School © 2012)

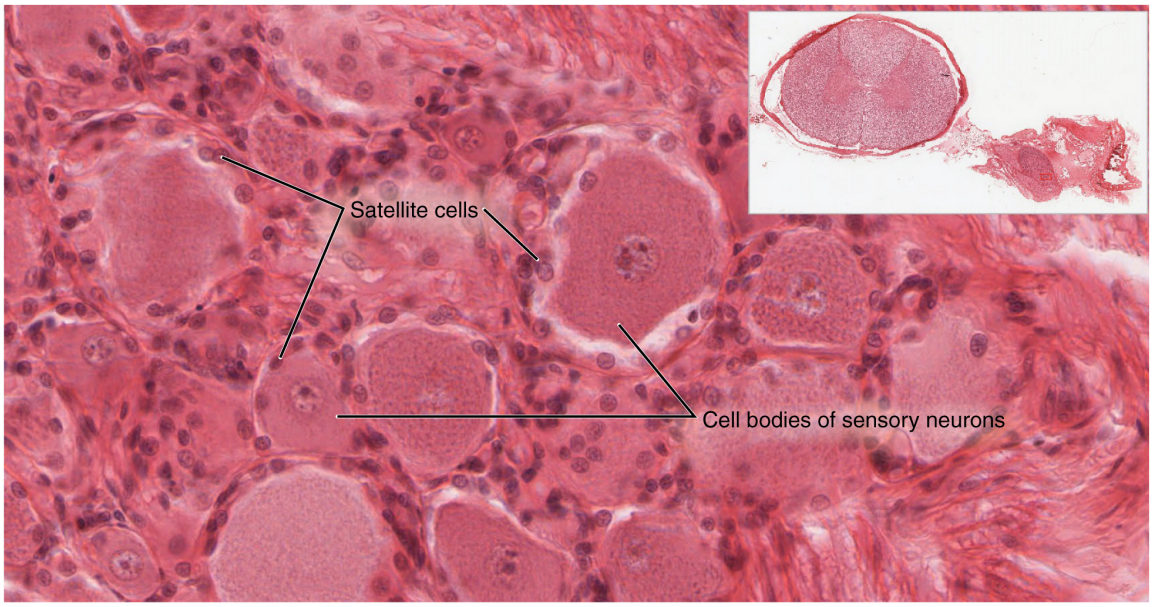


FIGURE 13.20 Spinal Cord and Root Ganglion The slide includes both a cross-section of the lumbar spinal cord and a section of the dorsal root ganglion (see also Figure 13.19) (tissue source: canine). LM × 1600. (Micrograph provided by the Regents of University of Michigan Medical School © 2012)

INTERACTIVE LINK

View the University of Michigan WebScope (http://openstax.org/l/spinalroot) to explore the tissue sample in greater detail. If you zoom in on the dorsal root ganglion, you can see smaller satellite glial cells surrounding the large cell bodies of the sensory neurons. From what structure do satellite cells derive during embryologic development?

Another type of sensory ganglion is a **cranial nerve ganglion**. This is analogous to the dorsal root ganglion, except that it is associated with a **cranial nerve** instead of a **spinal nerve**. The roots of cranial nerves are within the cranium, whereas the ganglia are outside the skull. For example, the **trigeminal ganglion** is superficial to the temporal bone whereas its associated nerve is attached to the mid-pons region of the brain stem. The neurons of

cranial nerve ganglia are also unipolar in shape with associated satellite cells.

The other major category of ganglia are those of the autonomic nervous system, which is divided into the sympathetic and parasympathetic nervous systems. The **sympathetic chain ganglia** constitute a row of ganglia along the vertebral column that receive central input from the lateral horn of the thoracic and upper lumbar spinal cord. Superior to the chain ganglia are three **paravertebral ganglia** in the cervical region. Three other autonomic ganglia that are related to the sympathetic chain are the **prevertebral ganglia**, which are located outside of the chain but have similar functions. They are referred to as prevertebral because they are anterior to the vertebral column. The neurons of these autonomic ganglia are multipolar in shape, with dendrites radiating out around the cell body where synapses from the spinal cord neurons are made. The neurons of the chain, paravertebral, and prevertebral ganglia then project to organs in the head and neck, thoracic, abdominal, and pelvic cavities to regulate the sympathetic aspect of homeostatic mechanisms.

Another group of autonomic ganglia are the **terminal ganglia** that receive input from cranial nerves or sacral spinal nerves and are responsible for regulating the parasympathetic aspect of homeostatic mechanisms. These two sets of ganglia, sympathetic and parasympathetic, often project to the same organs—one input from the chain ganglia and one input from a terminal ganglion—to regulate the overall function of an organ. For example, the heart receives two inputs such as these; one increases heart rate, and the other decreases it. The terminal ganglia that receive input from cranial nerves are found in the head and neck, as well as the thoracic and upper abdominal cavities, whereas the terminal ganglia that receive sacral input are in the lower abdominal and pelvic cavities.

Terminal ganglia below the head and neck are often incorporated into the wall of the target organ as a **plexus**. A plexus, in a general sense, is a network of fibers or vessels. This can apply to nervous tissue (as in this instance) or structures containing blood vessels (such as a choroid plexus). For example, the **enteric plexus** is the extensive network of axons and neurons in the wall of the small and large intestines. The enteric plexus is actually part of the enteric nervous system, along with the **gastric plexuses** and the **esophageal plexus**. Though the enteric nervous system receives input originating from central neurons of the autonomic nervous system, it does not require CNS input to function. In fact, it operates independently to regulate the digestive system.

Nerves

Bundles of axons in the PNS are referred to as nerves. These structures in the periphery are different than the central counterpart, called a tract. Nerves are composed of more than just nervous tissue. They have connective tissues invested in their structure, as well as blood vessels supplying the tissues with nourishment. The outer surface of a nerve is a surrounding layer of fibrous connective tissue called the **epineurium**. Within the nerve, axons are further bundled into **fascicles**, which are each surrounded by their own layer of fibrous connective tissue called **perineurium**. Finally, individual axons are surrounded by loose connective tissue called the **endoneurium** (Figure 13.21). These three layers are similar to the connective tissue sheaths for muscles. Nerves are associated with the region of the CNS to which they are connected, either as cranial nerves connected to the brain or spinal nerves connected to the spinal cord.

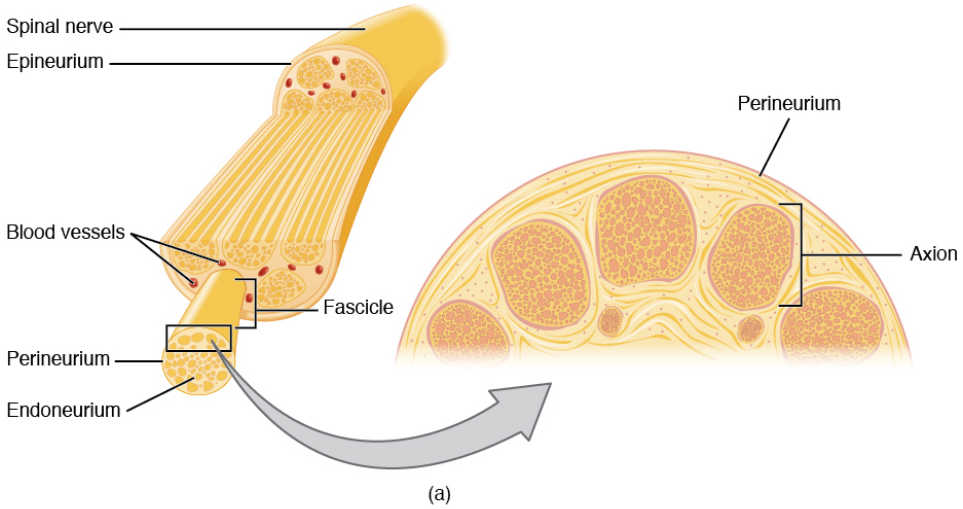


FIGURE 13.21 **Nerve Structure** The structure of a nerve is organized by the layers of connective tissue on the outside, around each fascicle, and surrounding the individual nerve fibers (tissue source: simian). LM × 40. (Micrograph provided by the Regents of University of Michigan Medical School © 2012)

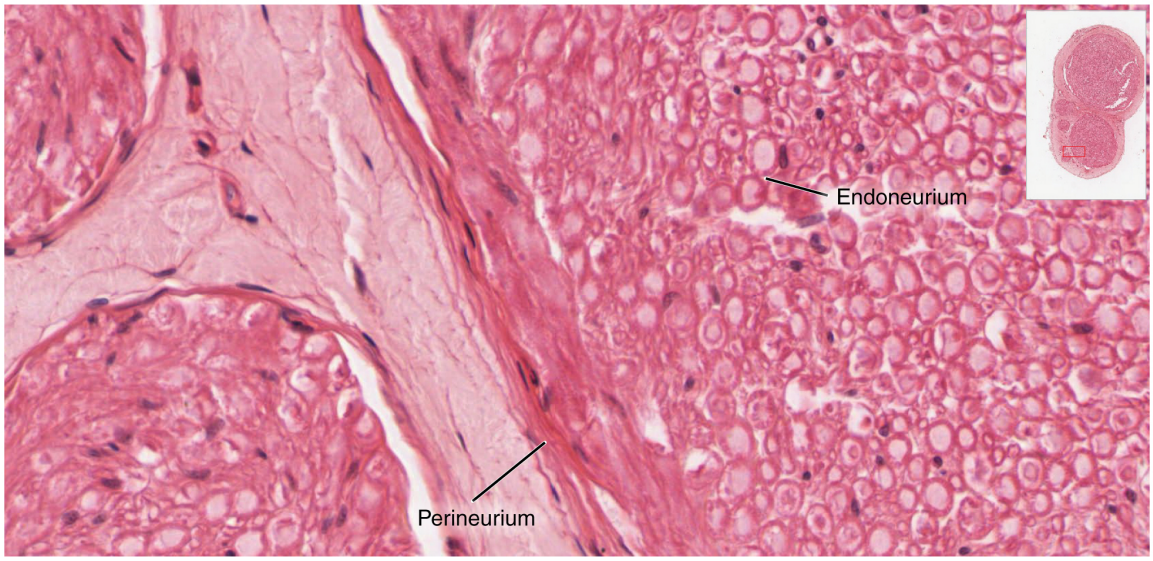


FIGURE 13.22 **Close-Up of Nerve Trunk** Zoom in on this slide of a nerve trunk to examine the endoneurium, perineurium, and

epineurium in greater detail (tissue source: simian). LM × 1600. (Micrograph provided by the Regents of University of Michigan Medical School © 2012)

INTERACTIVE LINK

View the University of Michigan WebScope (http://openstax.org/l/nervetrunk) to explore the tissue sample in greater detail. With what structures in a skeletal muscle are the endoneurium, perineurium, and epineurium comparable?

Cranial Nerves

The nerves attached to the brain are the cranial nerves, which are primarily responsible for the sensory and motor functions of the head and neck (one of these nerves targets organs in the thoracic and abdominal cavities as part of the parasympathetic nervous system). There are twelve cranial nerves, which are designated CNI through CNXII for "Cranial Nerve," using Roman numerals for 1 through 12. They can be classified as sensory nerves, motor nerves, or a combination of both, meaning that the axons in these nerves originate out of sensory ganglia external to the cranium or motor nuclei within the brain stem. Sensory axons enter the brain to synapse in a nucleus. Motor axons connect to skeletal muscles of the head or neck. Three of the nerves are solely composed of sensory fibers; five are strictly motor; and the remaining four are mixed nerves.

Learning the cranial nerves is a tradition in anatomy courses, and students have always used mnemonic devices to remember the nerve names. A traditional mnemonic is the rhyming couplet, "On Old Olympus' Towering Tops/A Finn And German Viewed Some Hops," in which the initial letter of each word corresponds to the initial letter in the name of each nerve. The names of the nerves have changed over the years to reflect current usage and more accurate naming. An exercise to help learn this sort of information is to generate a mnemonic using words that have personal significance. The names of the cranial nerves are listed in Table 13.3 along with a brief description of their function, their source (sensory ganglion or motor nucleus), and their target (sensory nucleus or skeletal muscle). They are listed here with a brief explanation of each nerve (Figure 13.23).

The **olfactory nerve** and **optic nerve** are responsible for the sense of smell and vision, respectively. The **oculomotor nerve** is responsible for eye movements by controlling four of the **extraocular muscles**. It is also responsible for lifting the upper eyelid when the eyes point up, and for pupillary constriction. The **trochlear nerve** and the **abducens nerve** are both responsible for eye movement, but do so by controlling different extraocular muscles. The **trigeminal nerve** is responsible for cutaneous sensations of the face and controlling the muscles of mastication. The **facial nerve** is responsible for the muscles involved in facial expressions, as well as part of the sense of taste and the production of saliva. The **vestibulocochlear nerve** is responsible for the senses of hearing and balance. The **glossopharyngeal nerve** is responsible for controlling muscles in the oral cavity and upper throat, as well as part of the sense of taste and the production of saliva. The **vagus nerve** is responsible for contributing to homeostatic control of the organs of the thoracic and upper abdominal cavities. The **spinal accessory nerve** is responsible for controlling the muscles of the neck, along with cervical spinal nerves. The **hypoglossal nerve** is responsible for controlling the muscles of the lower throat and tongue.

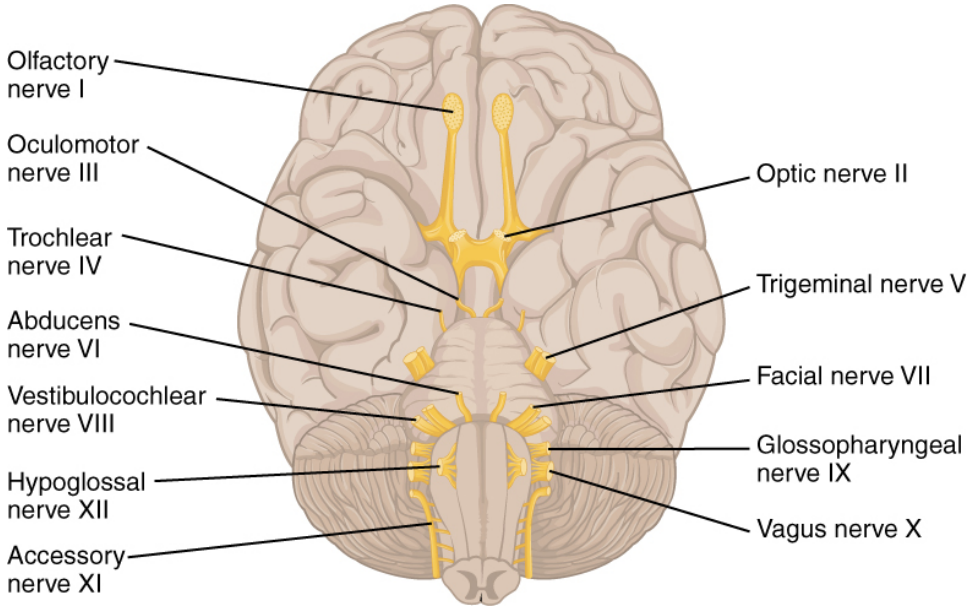


FIGURE 13.23 The Cranial Nerves The anatomical arrangement of the roots of the cranial nerves observed from an inferior view of the brain.

Three of the cranial nerves also contain autonomic fibers, and a fourth is almost purely a component of the autonomic system. The oculomotor, facial, and glossopharyngeal nerves contain fibers that contact autonomic ganglia. The oculomotor fibers initiate pupillary constriction, whereas the facial and glossopharyngeal fibers both initiate salivation. The vagus nerve primarily targets autonomic ganglia in the thoracic and upper abdominal cavities.

INTERACTIVE LINK

Visit this site (http://openstax.org/l/NYTmeningitis) to read about a man who wakes with a headache and a loss of vision. His regular doctor sent him to an ophthalmologist to address the vision loss. The ophthalmologist recognizes a greater problem and immediately sends him to the emergency room. Once there, the patient undergoes a large battery of tests, but a definite cause cannot be found. A specialist recognizes the problem as meningitis, but the question is what caused it originally. How can that be cured? The loss of vision comes from swelling around the optic nerve, which probably presented as a bulge on the inside of the eye. Why is swelling related to meningitis going to push on the optic nerve?

Another important aspect of the cranial nerves that lends itself to a mnemonic is the functional role each nerve plays. The nerves fall into one of three basic groups. They are sensory, motor, or both (see Table 13.3). The sentence, “Some Say Marry Money But My Brother Says Brains Beauty Matter More,” corresponds to the basic function of each nerve. The first, second, and eighth nerves are purely sensory: the olfactory (CNI), optic (CNII), and vestibulocochlear (CNVIII) nerves. The three eye-movement nerves are all motor: the oculomotor (CNIII), trochlear (CNIV), and abducens (CNVI). The spinal accessory (CNXI) and hypoglossal (CNXII) nerves are also strictly motor. The remainder of the nerves contain both sensory and motor fibers. They are the trigeminal (CNV), facial (CNVII), glossopharyngeal (CNIX), and vagus (CNX) nerves. The nerves that convey both are often related to each other. The trigeminal and facial nerves both concern the face; one concerns the sensations and the other concerns the muscle movements. The facial and glossopharyngeal nerves are both responsible for conveying gustatory, or taste, sensations as well as controlling salivary glands. The vagus nerve is involved in visceral responses to taste, namely the gag reflex. This is not an exhaustive list of what these combination nerves do, but there is a thread of relation between them.

Cranial Nerves

Mnemonic	#	Name	Function (S/M/B)	Central connection (nuclei)	Peripheral connection (ganglion or muscle)
On	I	Olfactory	Smell (S)	Olfactory bulb	Olfactory epithelium
Old	II	Optic	Vision (S)	Hypothalamus/ thalamus/midbrain	Retina (retinal ganglion cells)
Olympus'	III	Oculomotor	Eye movements (M)	Oculomotor nucleus	Extraocular muscles (other 4), levator palpebrae superioris, ciliary ganglion (autonomic)
Towering	IV	Trochlear	Eye movements (M)	Trochlear nucleus	Superior oblique muscle
Tops	V	Trigeminal	Sensory/ motor – face (B)	Trigeminal nuclei in the midbrain, pons, and medulla	Trigeminal
A	VI	Abducens	Eye movements (M)	Abducens nucleus	Lateral rectus muscle
Finn	VII	Facial	Motor – face, Taste (B)	Facial nucleus, solitary nucleus, superior salivatory nucleus	Facial muscles, Geniculate ganglion, Pterygopalatine ganglion (autonomic)
And	VIII	Auditory (Vestibulocochlear)	Hearing/ balance (S)	Cochlear nucleus, Vestibular nucleus/ cerebellum	Spiral ganglion (hearing), Vestibular ganglion (balance)
German	IX	Glossopharyngeal	Motor – throat Taste (B)	Solitary nucleus, inferior salivatory nucleus, nucleus ambiguus	Pharyngeal muscles, Geniculate ganglion, Otic ganglion (autonomic)
Viewed	X	Vagus	Motor/ sensory – viscera (autonomic) (B)	Medulla	Terminal ganglia serving thoracic and upper abdominal organs (heart and small intestines)

TABLE 13.3

Mnemonic	#	Name	Function (S/M/B)	Central connection (nuclei)	Peripheral connection (ganglion or muscle)
Some	XI	Spinal Accessory	Motor – head and neck (M)	Spinal accessory nucleus	Neck muscles
Hops	XII	Hypoglossal	Motor – lower throat (M)	Hypoglossal nucleus	Muscles of the larynx and lower pharynx

TABLE 13.3

Spinal Nerves

The nerves connected to the spinal cord are the spinal nerves. The arrangement of these nerves is much more regular than that of the cranial nerves. All of the spinal nerves are combined sensory and motor axons that separate into two nerve roots. The sensory axons enter the spinal cord as the dorsal nerve root. The motor fibers, both somatic and autonomic, emerge as the ventral nerve root. The dorsal root ganglion for each nerve is an enlargement of the spinal nerve.

There are 31 spinal nerves, named for the level of the spinal cord at which each one emerges. There are eight pairs of cervical nerves designated C1 to C8, twelve thoracic nerves designated T1 to T12, five pairs of lumbar nerves designated L1 to L5, five pairs of sacral nerves designated S1 to S5, and one pair of coccygeal nerves. The nerves are numbered from the superior to inferior positions, and each emerges from the vertebral column through the intervertebral foramen at its level. The first nerve, C1, emerges between the first cervical vertebra and the occipital bone. The second nerve, C2, emerges between the first and second cervical vertebrae. The same occurs for C3 to C7, but C8 emerges between the seventh cervical vertebra and the first thoracic vertebra. For the thoracic and lumbar nerves, each one emerges between the vertebra that has the same designation and the next vertebra in the column. The sacral nerves emerge from the sacral foramina along the length of that unique vertebra.

Spinal nerves extend outward from the vertebral column to innervate the periphery. The nerves in the periphery are not straight continuations of the spinal nerves, but rather the reorganization of the axons in those nerves to follow different courses. Axons from different spinal nerves will come together into a **systemic nerve**. This occurs at four places along the length of the vertebral column, each identified as a **nerve plexus**, whereas the other spinal nerves directly correspond to nerves at their respective levels. In this instance, the word plexus is used to describe networks of nerve fibers with no associated cell bodies.

Of the four nerve plexuses, two are found at the cervical level, one at the lumbar level, and one at the sacral level (Figure 13.24). The **cervical plexus** is composed of axons from spinal nerves C1 through C5 and branches into nerves in the posterior neck and head, as well as the **phrenic nerve**, which connects to the diaphragm at the base of the thoracic cavity. The other plexus from the cervical level is the **brachial plexus**. Spinal nerves C4 through T1 reorganize through this plexus to give rise to the nerves of the arms, as the name brachial suggests. A large nerve from this plexus is the **radial nerve** from which the **axillary nerve** branches to go to the armpit region. The radial nerve continues through the arm and is paralleled by the **ulnar nerve** and the **median nerve**. The **lumbar plexus** arises from all the lumbar spinal nerves and gives rise to nerves enervating the pelvic region and the anterior leg. The **femoral nerve** is one of the major nerves from this plexus, which gives rise to the **saphenous nerve** as a branch that extends through the anterior lower leg. The **sacral plexus** comes from the lower lumbar nerves L4 and L5 and the sacral nerves S1 to S4. The most significant systemic nerve to come from this plexus is the **sciatic nerve**, which is a combination of the **tibial nerve** and the **fibular nerve**. The sciatic nerve extends across the hip joint and is most commonly associated with the condition **sciatica**, which is the result of compression or irritation of the nerve or any of the spinal nerves giving rise to it.

These plexuses are described as arising from spinal nerves and giving rise to certain systemic nerves, but they contain fibers that serve sensory functions or fibers that serve motor functions. This means that some fibers extend from cutaneous or other peripheral sensory surfaces and send action potentials into the CNS. Those are axons of

sensory neurons in the dorsal root ganglia that enter the spinal cord through the dorsal nerve root. Other fibers are the axons of motor neurons of the anterior horn of the spinal cord, which emerge in the ventral nerve root and send action potentials to cause skeletal muscles to contract in their target regions. For example, the radial nerve contains fibers of cutaneous sensation in the arm, as well as motor fibers that move muscles in the arm.

Spinal nerves of the thoracic region, T2 through T11, are not part of the plexuses but rather emerge and give rise to the **intercostal nerves** found between the ribs, which articulate with the vertebrae surrounding the spinal nerve.

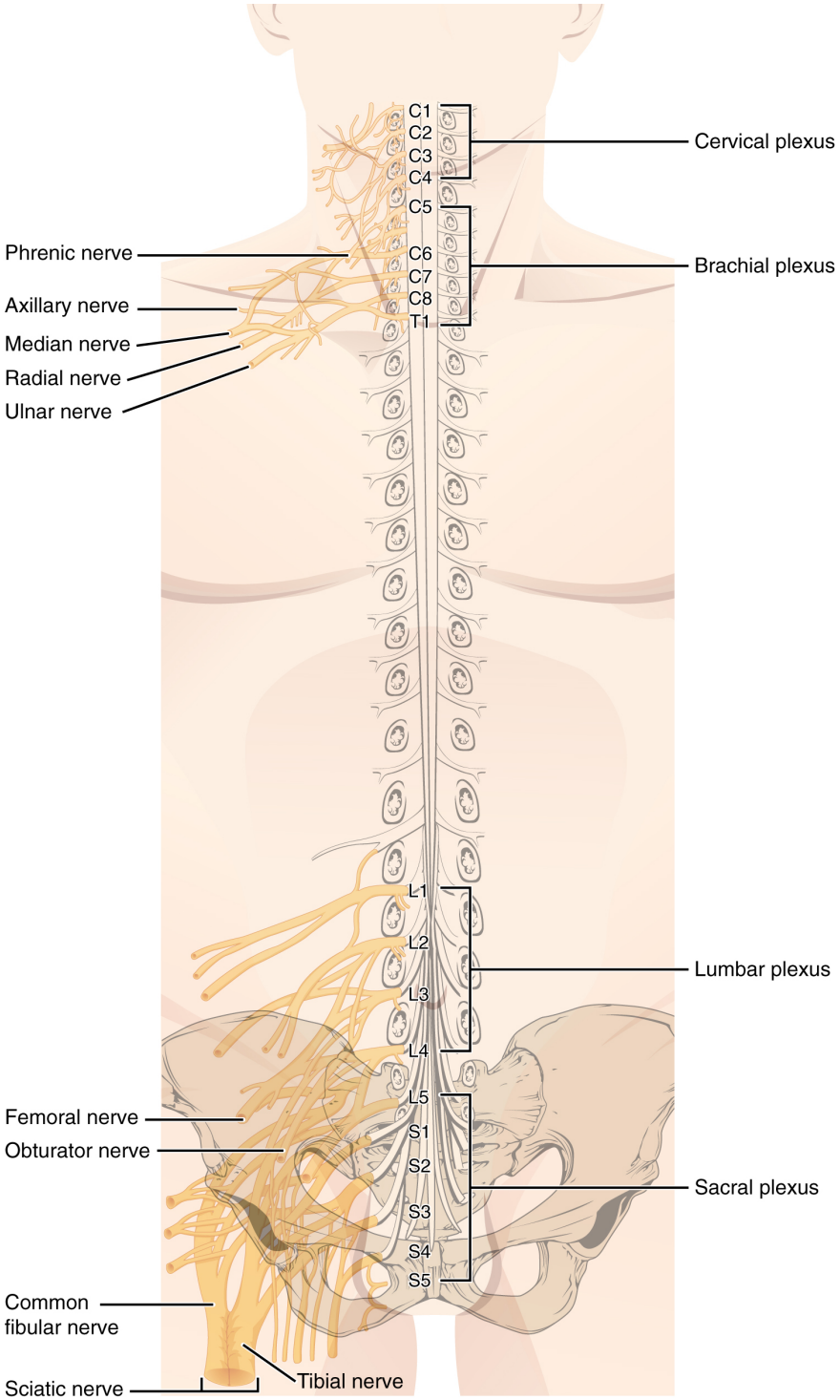


FIGURE 13.24 **Nerve Plexuses of the Body** There are four main nerve plexuses in the human body. The cervical plexus supplies nerves to the posterior head and neck, as well as to the diaphragm. The brachial plexus supplies nerves to the arm. The lumbar plexus supplies nerves to the anterior leg. The sacral plexus supplies nerves to the posterior leg.

Aging and the...

Nervous System

Anosmia is the loss of the sense of smell. It is often the result of the olfactory nerve being severed, usually because of blunt force trauma to the head. The sensory neurons of the olfactory epithelium have a limited lifespan of approximately one to four months, and new ones are made on a regular basis. The new neurons extend their axons into the CNS by growing along the existing fibers of the olfactory nerve. The ability of these neurons to be replaced is lost with age. Age-related anosmia is not the result of impact trauma to the head, but rather a slow loss of the sensory neurons with no new neurons born to replace them.

Smell is an important sense, especially for the enjoyment of food. There are only five tastes sensed by the tongue, and two of them are generally thought of as unpleasant tastes (sour and bitter). The rich sensory experience of food is the result of odor molecules associated with the food, both as food is moved into the mouth, and therefore passes under the nose, and when it is chewed and molecules are released to move up the pharynx into the posterior nasal cavity. Anosmia results in a loss of the enjoyment of food.

As the replacement of olfactory neurons declines with age, anosmia can set in. Without the sense of smell, many sufferers complain of food tasting bland. Often, the only way to enjoy food is to add seasoning that can be sensed on the tongue, which usually means adding table salt. The problem with this solution, however, is that this increases sodium intake, which can lead to cardiovascular problems through water retention and the associated increase in blood pressure.

Key Terms

abducens nerve sixth cranial nerve; responsible for contraction of one of the extraocular muscles

alar plate developmental region of the spinal cord that gives rise to the posterior horn of the gray matter

amygdala nucleus deep in the temporal lobe of the cerebrum that is related to memory and emotional behavior

anterior column white matter between the anterior horns of the spinal cord composed of many different groups of axons of both ascending and descending tracts

anterior horn gray matter of the spinal cord containing multipolar motor neurons, sometimes referred to as the ventral horn

anterior median fissure deep midline feature of the anterior spinal cord, marking the separation between the right and left sides of the cord

anterior spinal artery blood vessel from the merged branches of the vertebral arteries that runs along the anterior surface of the spinal cord

arachnoid granulation outpocket of the arachnoid membrane into the dural sinuses that allows for reabsorption of CSF into the blood

arachnoid mater middle layer of the meninges named for the spider-web–like trabeculae that extend between it and the pia mater

arachnoid trabeculae filaments between the arachnoid and pia mater within the subarachnoid space

ascending tract central nervous system fibers carrying sensory information from the spinal cord or periphery to the brain

axillary nerve systemic nerve of the arm that arises from the brachial plexus

basal forebrain nuclei of the cerebrum related to modulation of sensory stimuli and attention through broad projections to the cerebral cortex, loss of which is related to Alzheimer's disease

basal nuclei nuclei of the cerebrum (with a few components in the upper brain stem and diencephalon) that are responsible for assessing cortical movement commands and comparing them with the general state of the individual through broad modulatory activity of dopamine neurons; largely related to motor functions, as evidenced through the symptoms of Parkinson's and Huntington's diseases

basal plate developmental region of the spinal cord that gives rise to the lateral and anterior horns of gray matter

basilar artery blood vessel from the merged vertebral arteries that runs along the dorsal surface of the brain stem

brachial plexus nerve plexus associated with the lower cervical spinal nerves and first thoracic spinal nerve

brain stem region of the adult brain that includes the midbrain, pons, and medulla oblongata and develops from the mesencephalon, metencephalon, and myelencephalon of the embryonic brain

Broca's area region of the frontal lobe associated with the motor commands necessary for speech production and located only in the cerebral hemisphere responsible for language production, which is the left side in approximately 95 percent of the population

Brodmann's areas mapping of regions of the cerebral cortex based on microscopic anatomy that relates specific areas to functional differences, as described by Brodmann in the early 1900s

carotid canal opening in the temporal bone through which the internal carotid artery enters the cranium

cauda equina bundle of spinal nerve roots that descend from the lower spinal cord below the first lumbar vertebra and lie within the vertebral cavity; has the appearance of a horse's tail

caudate nucleus deep in the cerebrum that is part of the basal nuclei; along with the putamen, it is part of the striatum

central canal hollow space within the spinal cord that is the remnant of the center of the neural tube

central sulcus surface landmark of the cerebral cortex that marks the boundary between the frontal and parietal lobes

cephalic flexure curve in midbrain of the embryo that positions the forebrain ventrally

cerebellum region of the adult brain connected primarily to the pons that developed from the metencephalon (along with the pons) and is largely responsible for comparing information from the cerebrum with sensory feedback from the periphery through the spinal cord

cerebral aqueduct connection of the ventricular system between the third and fourth ventricles located in the midbrain

cerebral cortex outer gray matter covering the forebrain, marked by wrinkles and folds known as gyri and sulci

cerebral hemisphere one half of the bilaterally symmetrical cerebrum

cerebrum region of the adult brain that develops from the telencephalon and is responsible for higher neurological functions such as memory, emotion,

and consciousness

cervical plexus nerve plexus associated with the upper cervical spinal nerves

choroid plexus specialized structures containing ependymal cells lining blood capillaries that filter blood to produce CSF in the four ventricles of the brain

circle of Willis unique anatomical arrangement of blood vessels around the base of the brain that maintains perfusion of blood into the brain even if one component of the structure is blocked or narrowed

common carotid artery blood vessel that branches off the aorta (or the brachiocephalic artery on the right) and supplies blood to the head and neck

corpus callosum large white matter structure that connects the right and left cerebral hemispheres

cranial nerve one of twelve nerves connected to the brain that are responsible for sensory or motor functions of the head and neck

cranial nerve ganglion sensory ganglion of cranial nerves

descending tract central nervous system fibers carrying motor commands from the brain to the spinal cord or periphery

diencephalon region of the adult brain that retains its name from embryonic development and includes the thalamus and hypothalamus

direct pathway connections within the basal nuclei from the striatum to the globus pallidus internal segment and substantia nigra pars reticulata that disinhibit the thalamus to increase cortical control of movement

disinhibition disynaptic connection in which the first synapse inhibits the second cell, which then stops inhibiting the final target

dorsal (posterior) nerve root axons entering the posterior horn of the spinal cord

dorsal (posterior) root ganglion sensory ganglion attached to the posterior nerve root of a spinal nerve

dura mater tough, fibrous, outer layer of the meninges that is attached to the inner surface of the cranium and vertebral column and surrounds the entire CNS

dural sinus any of the venous structures surrounding the brain, enclosed within the dura mater, which drain blood from the CNS to the common venous return of the jugular veins

endoneurium innermost layer of connective tissue that surrounds individual axons within a nerve

enteric nervous system peripheral structures, namely ganglia and nerves, that are incorporated into the digestive system organs

enteric plexus neuronal plexus in the wall of the intestines, which is part of the enteric nervous system

epineurium outermost layer of connective tissue that surrounds an entire nerve

epithalamus region of the diecephalon containing the pineal gland

esophageal plexus neuronal plexus in the wall of the esophagus that is part of the enteric nervous system

extraocular muscles six skeletal muscles that control eye movement within the orbit

facial nerve seventh cranial nerve; responsible for contraction of the facial muscles and for part of the sense of taste, as well as causing saliva production

fascicle small bundles of nerve or muscle fibers enclosed by connective tissue

femoral nerve systemic nerve of the anterior leg that arises from the lumbar plexus

fibular nerve systemic nerve of the posterior leg that begins as part of the sciatic nerve

foramen magnum large opening in the occipital bone of the skull through which the spinal cord emerges and the vertebral arteries enter the cranium

forebrain anterior region of the adult brain that develops from the prosencephalon and includes the cerebrum and diencephalon

fourth ventricle the portion of the ventricular system that is in the region of the brain stem and opens into the subarachnoid space through the median and lateral apertures

frontal eye field region of the frontal lobe associated with motor commands to orient the eyes toward an object of visual attention

frontal lobe region of the cerebral cortex directly beneath the frontal bone of the cranium

gastric plexuses neuronal networks in the wall of the stomach that are part of the enteric nervous system

globus pallidus nuclei deep in the cerebrum that are part of the basal nuclei and can be divided into the internal and external segments

glossopharyngeal nerve ninth cranial nerve; responsible for contraction of muscles in the tongue and throat and for part of the sense of taste, as well as causing saliva production

gyrus ridge formed by convolutions on the surface of the cerebrum or cerebellum

hindbrain posterior region of the adult brain that develops from the rhombencephalon and includes the pons, medulla oblongata, and cerebellum

hippocampus gray matter deep in the temporal lobe that is very important for long-term memory formation

hypoglossal nerve twelfth cranial nerve; responsible for contraction of muscles of the tongue
hypothalamus major region of the diencephalon that is responsible for coordinating autonomic and endocrine control of homeostasis
indirect pathway connections within the basal nuclei from the striatum through the globus pallidus external segment and subthalamic nucleus to the globus pallidus internal segment/substantia nigra pars compacta that result in inhibition of the thalamus to decrease cortical control of movement
inferior colliculus half of the midbrain tectum that is part of the brain stem auditory pathway
inferior olive nucleus in the medulla that is involved in processing information related to motor control
intercostal nerve systemic nerve in the thoracic cavity that is found between two ribs
internal carotid artery branch from the common carotid artery that enters the cranium and supplies blood to the brain
interventricular foramina openings between the lateral ventricles and third ventricle allowing for the passage of CSF
jugular veins blood vessels that return "used" blood from the head and neck
kinesthesia general sensory perception of movement of the body
lateral apertures pair of openings from the fourth ventricle to the subarachnoid space on either side and between the medulla and cerebellum
lateral column white matter of the spinal cord between the posterior horn on one side and the axons from the anterior horn on the same side; composed of many different groups of axons, of both ascending and descending tracts, carrying motor commands to and from the brain
lateral horn region of the spinal cord gray matter in the thoracic, upper lumbar, and sacral regions that is the central component of the sympathetic division of the autonomic nervous system
lateral sulcus surface landmark of the cerebral cortex that marks the boundary between the temporal lobe and the frontal and parietal lobes
lateral ventricles portions of the ventricular system that are in the region of the cerebrum
limbic cortex collection of structures of the cerebral cortex that are involved in emotion, memory, and behavior and are part of the larger limbic system
limbic system structures at the edge (limit) of the boundary between the forebrain and hindbrain that are most associated with emotional behavior and memory formation
longitudinal fissure large separation along the midline between the two cerebral hemispheres
lumbar plexus nerve plexus associated with the lumbar spinal nerves
lumbar puncture procedure used to withdraw CSF from the lower lumbar region of the vertebral column that avoids the risk of damaging CNS tissue because the spinal cord ends at the upper lumbar vertebrae
median aperture singular opening from the fourth ventricle into the subarachnoid space at the midline between the medulla and cerebellum
median nerve systemic nerve of the arm, located between the ulnar and radial nerves
meninges protective outer coverings of the CNS composed of connective tissue
mesencephalon primary vesicle of the embryonic brain that does not significantly change through the rest of embryonic development and becomes the midbrain
metencephalon secondary vesicle of the embryonic brain that develops into the pons and the cerebellum
midbrain middle region of the adult brain that develops from the mesencephalon
myelencephalon secondary vesicle of the embryonic brain that develops into the medulla
nerve plexus network of nerves without neuronal cell bodies included
neural crest tissue that detaches from the edges of the neural groove and migrates through the embryo to develop into peripheral structures of both nervous and non-nervous tissues
neural fold elevated edge of the neural groove
neural groove region of the neural plate that folds into the dorsal surface of the embryo and closes off to become the neural tube
neural plate thickened layer of neuroepithelium that runs longitudinally along the dorsal surface of an embryo and gives rise to nervous system tissue
neural tube precursor to structures of the central nervous system, formed by the invagination and separation of neuroepithelium
neuraxis central axis to the nervous system, from the posterior to anterior ends of the neural tube; the inferior tip of the spinal cord to the anterior surface of the cerebrum
occipital lobe region of the cerebral cortex directly beneath the occipital bone of the cranium
occipital sinuses dural sinuses along the edge of the occipital lobes of the cerebrum
oculomotor nerve third cranial nerve; responsible for contraction of four of the extraocular muscles, the muscle in the upper eyelid, and pupillary

constriction

olfaction special sense responsible for smell, which has a unique, direct connection to the cerebrum

olfactory nerve first cranial nerve; responsible for the sense of smell

optic nerve second cranial nerve; responsible for visual sensation

orthostatic reflex sympathetic function that maintains blood pressure when standing to offset the increased effect of gravity

paravertebral ganglia autonomic ganglia superior to the sympathetic chain ganglia

parietal lobe region of the cerebral cortex directly beneath the parietal bone of the cranium

parieto-occipital sulcus groove in the cerebral cortex representing the border between the parietal and occipital cortices

perineurium layer of connective tissue surrounding fascicles within a nerve

phrenic nerve systemic nerve from the cervical plexus that innervates the diaphragm

pia mater thin, innermost membrane of the meninges that directly covers the surface of the CNS

plexus network of nerves or nervous tissue

postcentral gyrus primary motor cortex located in the frontal lobe of the cerebral cortex

posterior columns white matter of the spinal cord that lies between the posterior horns of the gray matter, sometimes referred to as the dorsal column; composed of axons of ascending tracts that carry sensory information up to the brain

posterior horn gray matter region of the spinal cord in which sensory input arrives, sometimes referred to as the dorsal horn

posterior median sulcus midline feature of the posterior spinal cord, marking the separation between right and left sides of the cord

posterolateral sulcus feature of the posterior spinal cord marking the entry of posterior nerve roots and the separation between the posterior and lateral columns of the white matter

precentral gyrus ridge just posterior to the central sulcus, in the parietal lobe, where somatosensory processing initially takes place in the cerebrum

prefrontal lobe specific region of the frontal lobe anterior to the more specific motor function areas, which can be related to the early planning of movements and intentions to the point of being personality-type functions

premotor area region of the frontal lobe responsible for planning movements that will be executed through the primary motor cortex

prevertebral ganglia autonomic ganglia that are anterior to the vertebral column and functionally related to the sympathetic chain ganglia

primary vesicle initial enlargements of the anterior neural tube during embryonic development that develop into the forebrain, midbrain, and hindbrain

proprioception general sensory perceptions providing information about location and movement of body parts; the “sense of the self”

prosencephalon primary vesicle of the embryonic brain that develops into the forebrain, which includes the cerebrum and diencephalon

putamen nucleus deep in the cerebrum that is part of the basal nuclei; along with the caudate, it is part of the striatum

radial nerve systemic nerve of the arm, the distal component of which is located near the radial bone

reticular formation diffuse region of gray matter throughout the brain stem that regulates sleep, wakefulness, and states of consciousness

rhombencephalon primary vesicle of the embryonic brain that develops into the hindbrain, which includes the pons, cerebellum, and medulla

sacral plexus nerve plexus associated with the lower lumbar and sacral spinal nerves

saphenous nerve systemic nerve of the lower anterior leg that is a branch from the femoral nerve

sciatic nerve systemic nerve from the sacral plexus that is a combination of the tibial and fibular nerves and extends across the hip joint and gluteal region into the upper posterior leg

sciatica painful condition resulting from inflammation or compression of the sciatic nerve or any of the spinal nerves that contribute to it

secondary vesicle five vesicles that develop from primary vesicles, continuing the process of differentiation of the embryonic brain

sigmoid sinuses dural sinuses that drain directly into the jugular veins

somatosensation general senses related to the body, usually thought of as the senses of touch, which would include pain, temperature, and proprioception

spinal accessory nerve eleventh cranial nerve; responsible for contraction of neck muscles

spinal nerve one of 31 nerves connected to the spinal cord

straight sinus dural sinus that drains blood from the deep center of the brain to collect with the other sinuses

striatum the caudate and putamen collectively, as part of the basal nuclei, which receive input from the cerebral cortex

subarachnoid space space between the arachnoid

mater and pia mater that contains CSF and the fibrous connections of the arachnoid trabeculae

subcortical nucleus all the nuclei beneath the cerebral cortex, including the basal nuclei and the basal forebrain

substantia nigra pars compacta nuclei within the basal nuclei that release dopamine to modulate the function of the striatum; part of the motor pathway

substantia nigra pars reticulata nuclei within the basal nuclei that serve as an output center of the nuclei; part of the motor pathway

subthalamus nucleus within the basal nuclei that is part of the indirect pathway

sulcus groove formed by convolutions in the surface of the cerebral cortex

superior colliculus half of the midbrain tectum that is responsible for aligning visual, auditory, and somatosensory spatial perceptions

superior sagittal sinus dural sinus that runs along the top of the longitudinal fissure and drains blood from the majority of the outer cerebrum

sympathetic chain ganglia autonomic ganglia in a chain along the anterolateral aspect of the vertebral column that are responsible for contributing to homeostatic mechanisms of the autonomic nervous system

systemic nerve nerve in the periphery distal to a nerve plexus or spinal nerve

tectum region of the midbrain, thought of as the roof of the cerebral aqueduct, which is subdivided into the inferior and superior colliculi

tegmentum region of the midbrain, thought of as the floor of the cerebral aqueduct, which continues into the pons and medulla as the floor of the fourth ventricle

telencephalon secondary vesicle of the embryonic brain that develops into the cerebrum

temporal lobe region of the cerebral cortex directly beneath the temporal bone of the cranium

terminal ganglion autonomic ganglia that are near or within the walls of organs that are responsible for contributing to homeostatic mechanisms of the autonomic nervous system

thalamus major region of the diencephalon that is responsible for relaying information between the cerebrum and the hindbrain, spinal cord, and periphery

third ventricle portion of the ventricular system that is in the region of the diencephalon

tibial nerve systemic nerve of the posterior leg that begins as part of the sciatic nerve

transverse sinuses dural sinuses that drain along either side of the occipital–cerebellar space

trigeminal ganglion sensory ganglion that contributes sensory fibers to the trigeminal nerve

trigeminal nerve fifth cranial nerve; responsible for cutaneous sensation of the face and contraction of the muscles of mastication

trochlear nerve fourth cranial nerve; responsible for contraction of one of the extraocular muscles

ulnar nerve systemic nerve of the arm located close to the ulna, a bone of the forearm

vagus nerve tenth cranial nerve; responsible for the autonomic control of organs in the thoracic and upper abdominal cavities

ventral (anterior) nerve root axons emerging from the anterior or lateral horns of the spinal cord

ventricles remnants of the hollow center of the neural tube that are spaces for cerebrospinal fluid to circulate through the brain

vertebral arteries arteries that ascend along either side of the vertebral column through the transverse foramina of the cervical vertebrae and enter the cranium through the foramen magnum

vestibulocochlear nerve eighth cranial nerve; responsible for the sensations of hearing and balance

Chapter Review

13.1 The Embryologic Perspective

The development of the nervous system starts early in embryonic development. The outer layer of the embryo, the ectoderm, gives rise to the skin and the nervous system. A specialized region of this layer, the neuroectoderm, becomes a groove that folds in and becomes the neural tube beneath the dorsal surface of the embryo. The anterior end of the neural tube develops into the brain, and the posterior region becomes the spinal cord. Tissues at the edges of the neural groove, when it closes off, are called the neural crest and migrate through the embryo to give rise to PNS structures as well as some non-nervous tissues.

The brain develops from this early tube structure and gives rise to specific regions of the adult brain. As the neural tube grows and differentiates, it enlarges into three vesicles that correspond to the forebrain, midbrain, and hindbrain regions of the adult brain. Later in development, two of these three vesicles differentiate further, resulting in five vesicles. Those five vesicles can be aligned with the four major regions of the adult brain. The cerebrum is formed directly from the telencephalon. The diencephalon is the only region that keeps its embryonic name. The

mesencephalon, metencephalon, and myelencephalon become the brain stem. The cerebellum also develops from the metencephalon and is a separate region of the adult brain.

The spinal cord develops out of the rest of the neural tube and retains the tube structure, with the nervous tissue thickening and the hollow center becoming a very small central canal through the cord. The rest of the hollow center of the neural tube corresponds to open spaces within the brain called the ventricles, where cerebrospinal fluid is found.

13.2 The Central Nervous System

The adult brain is separated into four major regions: the cerebrum, the diencephalon, the brain stem, and the cerebellum. The cerebrum is the largest portion and contains the cerebral cortex and subcortical nuclei. It is divided into two halves by the longitudinal fissure.

The cortex is separated into the frontal, parietal, temporal, and occipital lobes. The frontal lobe is responsible for motor functions, from planning movements through executing commands to be sent to the spinal cord and periphery. The most anterior portion of the frontal lobe is the prefrontal cortex, which is associated with aspects of personality through its influence on motor responses in decision-making.

The other lobes are responsible for sensory functions. The parietal lobe is where somatosensation is processed. The occipital lobe is where visual processing begins, although the other parts of the brain can contribute to visual function. The temporal lobe contains the cortical area for auditory processing, but also has regions crucial for memory formation.

Nuclei beneath the cerebral cortex, known as the subcortical nuclei, are responsible for augmenting cortical functions. The basal nuclei receive input from cortical areas and compare it with the general state of the individual through the activity of a dopamine-releasing nucleus. The output influences the activity of part of the thalamus that can then increase or decrease cortical activity that often results in changes to motor commands. The basal forebrain is responsible for modulating cortical activity in attention and memory. The limbic system includes deep cerebral nuclei that are responsible for emotion and memory.

The diencephalon includes the thalamus and the hypothalamus, along with some other structures. The thalamus is a relay between the cerebrum and the rest of the nervous system. The hypothalamus coordinates homeostatic functions through the autonomic and endocrine systems.

The brain stem is composed of the midbrain, pons, and medulla. It controls the head and neck region of the body through the cranial nerves. There are control centers in the brain stem that regulate the cardiovascular and respiratory systems.

The cerebellum is connected to the brain stem, primarily at the pons, where it receives a copy of the descending input from the cerebrum to the spinal cord. It can compare this with sensory feedback input through the medulla and send output through the midbrain that can correct motor commands for coordination.

13.3 Circulation and the Central Nervous System

The CNS has a privileged blood supply established by the blood-brain barrier. Establishing this barrier are anatomical structures that help to protect and isolate the CNS. The arterial blood to the brain comes from the internal carotid and vertebral arteries, which both contribute to the unique circle of Willis that provides constant perfusion of the brain even if one of the blood vessels is blocked or narrowed. That blood is eventually filtered to make a separate medium, the CSF, that circulates within the spaces of the brain and then into the surrounding space defined by the meninges, the protective covering of the brain and spinal cord.

The blood that nourishes the brain and spinal cord is behind the glial-cell–enforced blood-brain barrier, which limits the exchange of material from blood vessels with the interstitial fluid of the nervous tissue. Thus, metabolic wastes are collected in cerebrospinal fluid that circulates through the CNS. This fluid is produced by filtering blood at the choroid plexuses in the four ventricles of the brain. It then circulates through the ventricles and into the subarachnoid space, between the pia mater and the arachnoid mater. From the arachnoid granulations, CSF is reabsorbed into the blood, removing the waste from the privileged central nervous tissue.

The blood, now with the reabsorbed CSF, drains out of the cranium through the dural sinuses. The dura mater is the tough outer covering of the CNS, which is anchored to the inner surface of the cranial and vertebral cavities. It surrounds the venous space known as the dural sinuses, which connect to the jugular veins, where blood drains from the head and neck.

13.4 The Peripheral Nervous System

The PNS is composed of the groups of neurons

(ganglia) and bundles of axons (nerves) that are outside of the brain and spinal cord. Ganglia are of two types, sensory or autonomic. Sensory ganglia contain unipolar sensory neurons and are found on the dorsal root of all spinal nerves as well as associated with many of the cranial nerves. Autonomic ganglia are in the sympathetic chain, the associated paravertebral or prevertebral ganglia, or in terminal ganglia near or within the organs controlled by the autonomic nervous system.

Nerves are classified as cranial nerves or spinal nerves on the basis of their connection to the brain or spinal cord, respectively. The twelve cranial nerves can be strictly sensory in function, strictly motor in function, or a combination of the two functions. Sensory fibers are axons of sensory ganglia that carry sensory information into the brain and target sensory nuclei. Motor fibers are axons of motor neurons in motor nuclei of the brain stem and target skeletal muscles of the head and neck. Spinal nerves are all mixed nerves with both sensory and motor fibers. Spinal nerves emerge from the spinal cord and reorganize through plexuses, which then give rise to systemic nerves. Thoracic spinal nerves are not part of any plexus, but give rise to the intercostal nerves directly.

Interactive Link Questions

1. Watch this animation (http://openstax.org/l/braindevel) to examine the development of the brain, starting with the neural tube. As the anterior end of the neural tube develops, it enlarges into the primary vesicles that establish the forebrain, midbrain, and hindbrain. Those structures continue to develop throughout the rest of embryonic development and into adolescence. They are the basis of the structure of the fully developed adult brain. How would you describe the difference in the relative sizes of the three regions of the brain when comparing the early (25th embryonic day) brain and the adult brain?
2. Watch this video (http://openstax.org/l/whitematter) to learn about the white matter in the cerebrum that develops during childhood and adolescence. This is a composite of MRI images taken of the brains of people from 5 years of age through 20 years of age, demonstrating how the cerebrum changes. As the color changes to blue, the ratio of gray matter to white matter changes. The caption for the video describes it as “less gray matter,” which is another way of saying “more white matter.” If the brain does not finish developing until approximately 20 years of age, can teenagers be held responsible for behaving badly?
3. Watch this video (http://openstax.org/l/basalnuclei1) to learn about the basal nuclei (also known as the basal ganglia), which have two pathways that process information within the cerebrum. As shown in this video, the direct pathway is the shorter pathway through the system that results in increased activity in the cerebral cortex and increased motor activity. The direct pathway is described as resulting in “disinhibition” of the thalamus. What does disinhibition mean? What are the two neurons doing individually to cause this?
4. Watch this video (http://openstax.org/l/basalnuclei2) to learn about the basal nuclei (also known as the basal ganglia), which have two pathways that process information within the cerebrum. As shown in this video, the indirect pathway is the longer pathway through the system that results in decreased activity in the cerebral cortex, and therefore less motor activity. The indirect pathway has an extra couple of connections in it, including disinhibition of the subthalamic nucleus. What is the end result on the thalamus, and therefore on movement initiated by the cerebral cortex?
5. Watch this video (http://openstax.org/l/graymatter) to learn about the gray matter of the spinal cord that receives input from fibers of the dorsal (posterior) root and sends information out through the fibers of the ventral (anterior) root. As discussed in this video, these connections represent the interactions of the CNS with peripheral structures for both sensory and motor functions. The cervical and lumbar spinal cords have enlargements as a result of larger populations of neurons. What are these enlargements responsible for?