1 The evolution of the pre-cognitive control of action

If you dropped a newborn infant into a swimming pool, do you think that it would swim? Remarkably, it would. A newborn infant cannot roll over and can barely manipulate its fingers. Yet, when placed in a pool, the infant swims both vigorously and happily. I can still remember the first time I saw this, in a grainy movie shown in an undergraduate developmental psychology class. It seemed almost too amazing to believe. I had to wait many years to confirm it, and then my son was born, and as soon as we got him home I took him to a pool, placed him in it, and let go. He swam from one end to the other. So, I can assure you from my own experience. Infants can swim!

Why infants can swim illuminates one of the important milestones in the evolution of cognition. The evolution of cognition begins with the control of action. Almost all animals, except for the very simplest, are born with a set of automatic responses to things they will encounter in the world. Though not of importance to human survival, the infant swim reflex is a reminder that we evolved from creatures for which automatic action was a larger portion of their behavior than it is of ours. Initially, the nervous system evolved to automatically control action. Little learning was possible and reasoning was unnecessary.

1.1 The control of action

Cognition evolved from the control of action. An **action** is the movement of a body part in response to some **target** perceived by an animal. So, falling off a cliff and being blown in the wind do not count as actions. Rather, action implies **sensation**, because the animal must be able to detect the stimulus that the action is in response to. If you cannot move about and have an effect on your place in the world then there is no value to you in perceiving and thinking about the world. That is why there is a psychology of animals but there is not a psychology of plants. There is no survival value in being able to perceive the world around you if you cannot respond to what you perceive. The sole purpose of cognition is to make action more effective (Barsalou, 2008).

Every action has two components: a stimulus from the world detected by an organism, and its response to it. So, action begins with the ability to respond to the world. The ability to respond to the world begins with the evolution of the nervous system, which made it possible to detect changes in the world and respond to them. The simplest responses are called reflexes.

Reflexes by themselves are not cognitive. They do not require thought. However, they were the important first step in the evolution of cognition. The neural mechanisms of reflexes formed the basis of the enhanced neural mechanisms that made cognition possible.

1.2 Reflexes

It is the nervous system that makes action possible. The simplest actions that an animal can produce regulate activities within the animal's own body. Life functions in all except the simplest animals are performed by several distinct systems. The digestive system breaks food down into nutrients, the respiratory system provides oxygen to burn them for energy, and the circulatory system delivers oxygen to all the cells of the body. These various systems do not function independently but are under the control of the **nervous system**, which regulates their activities to make them more effective. For example, the nervous system regulates heartbeat, stomach movements, contractions of the bladder and rectum, and secretions of glands.

The simplest form of action is the reflex, in which a stimulus elicits a response. All reflexes are performed by a sequence of neurons called the **reflex arc**, which begins with a sensory neuron and ends with a response neuron. A **sensory neuron** detects a change in the environment or in the animal itself, and a **response neuron** activates a muscle (or gland) in response to it. The other neurons in the arc, whose function is to transmit a signal from the sensory neuron to the response neuron, are called interneurons (Figure 1.1). Interneurons connect stimulus neurons to response neurons in complex patterns that combine many simpler reflexes into sophisticated responses to the world.

Each neuron is separated from the next neuron in the circuit by a small gap called a **synapse.** Because they are impossible to draw correctly in detail, illustrations such as Figure 1.1 and schematic diagrams of the neural mechanisms of reflexes are always misleading. Reflex arcs do not consist of one sensory neuron and one response neuron. Rather, they consist of hundreds of sensory and response neurons. Thousands of sensory–response neuron pairings are included in the arc; that is, each of the hundreds of sensory neurons forms synapses with each of the hundreds of response neurons, and vice versa.

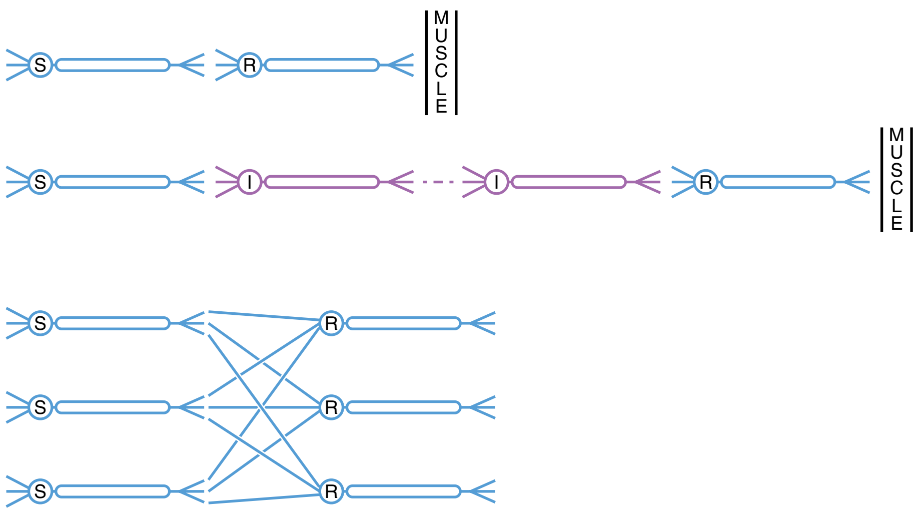

Figure 1.1 The reflex arc from a sensory neuron (S) to a response neuron (R) may consist of only those two neurons or the pathway may also contain one or more interneurons (top). Even the simplest reflex arc contains hundreds of sensory and response neurons and thousands of synapses between different pairs of neurons (bottom).

Most neurons communicate with the adjacent neuron by releasing a chemical signal called a **neurotransmitter**, which floats across the synapse and is taken up by the next neuron and stimulates it. (Some interneurons communicate by generating an electrical charge in the gap between them, but their function is not well understood: (Apostolides and Trussell, 2013.)

Many reflexes respond to stimulation from the environment. For example (as the great physiologist Ivan Pavlov discovered), placing a small amount of meat in a dog's mouth causes it to salivate, which begins the process of digesting the meat. The **pupillary light reflex** varies the size of the pupil so that the right amount of light for vision enters the eye. The **accommodation reflex** varies the shape of the eyeball so that the image projected on the retina is not blurred. In addition to regulating purely life functions through simple actions, reflexes evolved to perform increasingly complex actions in response to stimuli in the animal's environment.

Reflexes are also called **unconditioned responses**, because of a mistranslation from Russian. Pavlov described reflexes as unconditional because the same stimulus always caused the same response regardless of other conditions; "unconditional" was mistranslated as "unconditioned." The same mistranslation has been extended to the stimulus of the reflex, which is called the **unconditioned stimulus**. In many texts, stimulus and response are simply referred to by the initials **US** and **UR**.

Motor neurons are response neurons that initiate muscle contraction or relaxation, producing body movement. For example, blowing a puff of air in someone's eye causes it to blink, thus protecting the eye from harm.

The sea snail

In the simplest creatures that have reflexes, the reflexes are the only kinds of actions that the creature performs. One such creature is the sea snail, *Aplysia*, shown in Figure 1.2. In the

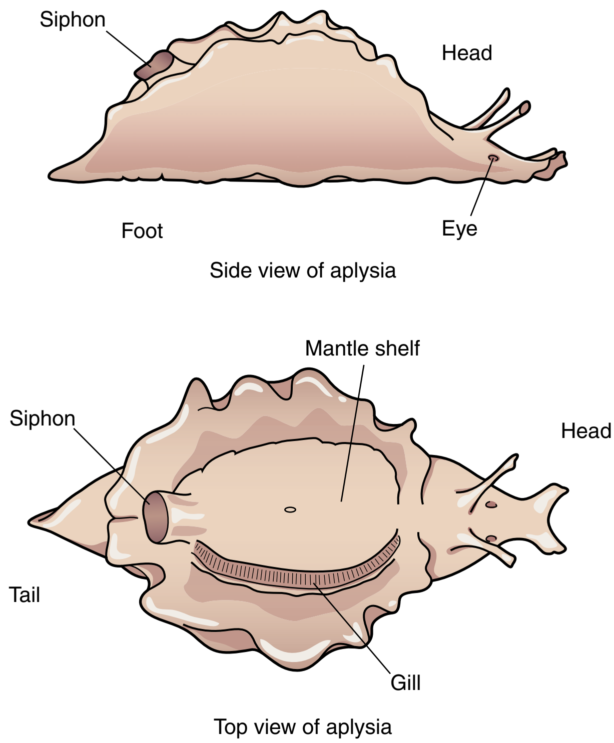

Figure 1.2 The siphon and gill are within the mantle cavity. When the siphon is touched, the entire gill withdraws into the mantle cavity for protection (Kandel, 2006).

Aplysia, six different reflexes, including the gill withdrawal reflex, are controlled by a group of 2,000 neurons (Kandel, 2006). As shown in the figure, in the top center of its body, called the mantle, there is an opening that contains its gill, which it breathes through, and its spout, through which it expels seawater and waste. Touching its siphon lightly produces a brisk defensive withdrawal of both the siphon and the gill.

The gill withdrawal reflex of the sea snail was studied intensively by Kandel (2006) because it had a nervous system that was simple enough that it appeared to be possible to figure out the neural mechanism that produced the reflexive movements in response to stimuli. It was expected that what was true of the neural mechanism producing reflexes in *Aplysia* would generally be true for the neural mechanisms of all animals with reflexes. This did turn out to be true, so the study of the neural mechanism of the reflexes of *Aplysia* was an extremely useful enterprise.

Neural mechanisms

The sensory neuron is separated from the response neuron by a small gap called a **synapse**. At the tips of the sensory neurons there are many tiny **terminal nodes**, which are containers filled with chemicals called **neurotransmitters**. When the sensory neuron is activated by a stimulus, its terminal nodes open and spill the neurotransmitter into the synapse, from which it is absorbed by receptors at the end of the response neuron. If the response neuron absorbs enough neurotransmitter, it becomes active and initiates the response. Kandel and his colleagues studied the neurons that were part of the neural pathway for the gill withdrawal reflex of *Aplysia*. They found that a single sensory neuron had about 1,300 terminal nodes, of which about 40 percent were active, contacting about twenty-five motor neurons; that is, about 40 percent spilled neurotransmitter into the synapse when the neuron was stimulated.

1.3 Habituation and sensitization

Despite Pavlov's characterization of reflexes as unconditional, the response to a repeated stimulus changes. Over successive repetitions, the strength of the response to a weak stimulus decreases and the strength of the response to a strong stimulus increases. These changes in response strength are called habituation and sensitization.

Functional characteristics

Habituation is when the response to a weak stimulus becomes weaker with each repetition of the weak stimulus. In this situation there may be complete habituation, so that eventually the response is not made at all. **Sensitization** is when the response to subsequent stimuli becomes stronger after a very strong stimulus is presented. Recall that touching an *Aplysia*'s siphon produces withdrawal of both the siphon and the gill. The force of the touch required varies with the experience of the individual snail. Repeated light touch produces **habituation** – that is, after each touch the withdrawal of the siphon is slower, until it doesn't withdraw at all. In contrast, a strong shock to either head or tail produces **sensitization** – that is, after the strong shock, a weak touch that previously did not cause the withdrawal of the siphon now does.

Habituation and sensitization adjust the strength and probability of a reflex to the current level of stimulation in the world around it. If the snail is pulling its way through some vegetation, it is counter-productive for it to withdraw into its shell every time it brushes against a leaf. Habituation decreases the sensitivity of the reflex to prevent this. On the other hand, the stronger the stimulus, the more potentially damaging it is. Sensitization increases the sensitivity of the reflex so that there is a fast and certain response to a potentially damaging stimulus.

How long the change in the sensitivity of the reflex persisted depended on the training routine to which the *Aplysia* was subjected. Carew and Kandel (1973), and their colleagues, found that forty weak electrical stimuli administered consecutively resulted in short-term habituation of the gill withdrawal that lasted only one day, but ten stimuli every day for four days produced long-term habituation that lasted for weeks. Similarly, Pinsker *et al*. (1973) found that four strong shocks on each of four successive days produced long-term sensitization that lasted for three weeks. The presentation of stimuli over a brief interval is called **massed** presentation. The presentation of stimuli over a long interval is called **distributed** or **spaced** presentation.

The short-term effect of massed training allows the creature to respond immediately to a current change in conditions. The long-term effect of distributed training allows the creature to adjust to a **routine** change in conditions. Thus, the neural mechanism makes sophisticated adjustments to changing conditions. Massed training is treated as the conditions of a single event, implying nothing about the future. Adjustments are short-term, hence temporary. Distributed training is treated as a repeated event, and the repeated event is treated as a routine event that may continue into the future. Hence, the adjustments are long-term and, given the continued routine, permanent.

The short-term versus long-term changes in siphon withdrawal are caused by different changes in the snail's nervous system. Short-term changes included the amount of neurotransmitter released into a synapse by the sensory neuron. Short-term habituation of the reflex occurred because, after each weak stimulus, the sensory neuron released less neurotransmitter into each synapse. Short-term sensitization of the reflex occurred because, after the strong stimulus, more neurotransmitter was released into each synapse. Such a short–term change had long been predicted by earlier investigators of the nervous system. However, it was the previously unknown, long-term changes in the neuron that were of particular interest. These demonstrated that, for even the simplest modification of action, the neural mechanisms were far more complicated than had been imagined.

Neural mechanisms of long-term changes in sensitivity

Recall that, in the gill withdrawal reflex, Kandel (2006) found that a single sensory neuron had approximately 1,300 pre-synaptic terminals, 40 percent of which were active, with which it contacted about 25 different motor neurons (Figure 1.3). This changed with both habituation and sensitization. In long-term habituation, the number of terminal nodes dropped to 850, of which 12 percent were active. In long-term sensitization, the number of terminal nodes increased to 2,700, of which 60 percent were active. In addition, there was outgrowth from the motor neuron to receive the output of the new terminals. Kandel suggested that, because building new terminals or removing old ones requires the availability of limited resources in the neurons, there could be only a limited decrease or increase in

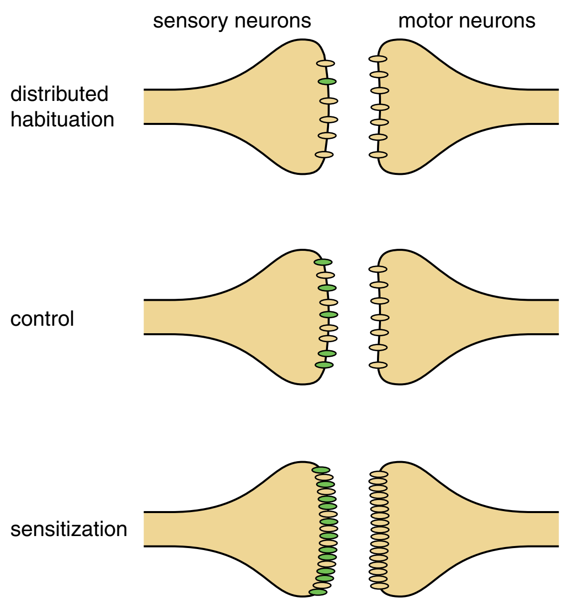

Figure 1.3 The number of terminal nodes on the presynaptic sensory neuron change as the result of distributed habituation (top) and distributed sensitization (bottom). Active nodes are shown darker. In sensitization, there is also a change in the number of post-synaptic receptor terminals (Kandel, 2006).

the number of terminals over a given training period regardless of the number of stimuli. Specifically, proteins used to make long-term changes in the cell take time to synthesize. Distributing the stimuli over a longer period of training results in more protein being available (Abbott and Kandel, 2012).

1.4 Complex reflexes and the organization of behavior

Animals do not perform individual voluntary actions independently of one another. Rather, as the result of evolution, they engage in behaviors such as foraging, stalking, chasing, feeding, and courting. A **behavior** consists of a sequence of complimentary actions towards a common purpose. Such behaviors may be complex, extended, reflexive responses in which earlier reflexes in the sequence generate stimuli that elicit later ones (Lorenz, 1958).

The aggregation of reflex arcs increased the sophistication of reflexive actions

To create more specific, precise, and effective responses, simpler reflex arcs were combined to generate more complex responses to more specific stimuli. For example, when a painful stimulus is applied to the foot of many animals, from amphibians such as frogs to mammals such as humans, there is a defensive withdrawal response (Tresilian, 2012). Precisely where the foot is touched determines the exact trajectory of its withdrawal movement in order to ensure that it no longer is in contact with the painful stimulus (Schouenborg, 2008). A stimulus may direct an action towards a target, as well as away from it. The wiping reflex of the frog will cause the leg to move into position and then wipe away an irritating particle. Again, the action is directed by an integrated set of reflexes that direct it to the irritating particle (Berkinblit, Feldman, and Fukson, 1986).

Furthermore, a pattern of stimuli may elicit a sequence of responses through feed-forward stimulation, in which each response becomes the stimulus for the next response in the sequence. Hence, reflexes may include complex behaviors such as locomotion and feeding. When the response has several components extended over time, it is called a **modal action pattern**. In a modal action pattern, the initiation of some reflexes results in feed-forward stimulation that initiates other reflexes that form part of the action pattern. For example, a bird that sees an egg (or egg-like object) just outside its nest will push it into the nest.

Reflexes in complex animals

In the life of an animal, stimuli do not randomly activate its reflexes independently of events in its world. If this were the case then the reflexes would have limited functional value. Rather, the stimuli are parts of larger events that are relevant to the life of a creature. For example, a stimulus activating the gill withdrawal reflex of a sea snail may be part of a larger event in which other parts of the creature are pelted, perhaps by rain, or by gravel, or by another creature. For another example, the stimulus activating salivation is almost always part of a larger event in which the animal eats and digests a meal.

In complex animals, reflexes do not operate independently of each other but either as components of complicated, sophisticated systems of voluntary action or as withdrawal responses that prevent inadvertent injury from voluntary action. Reflexes consist of **cranial**

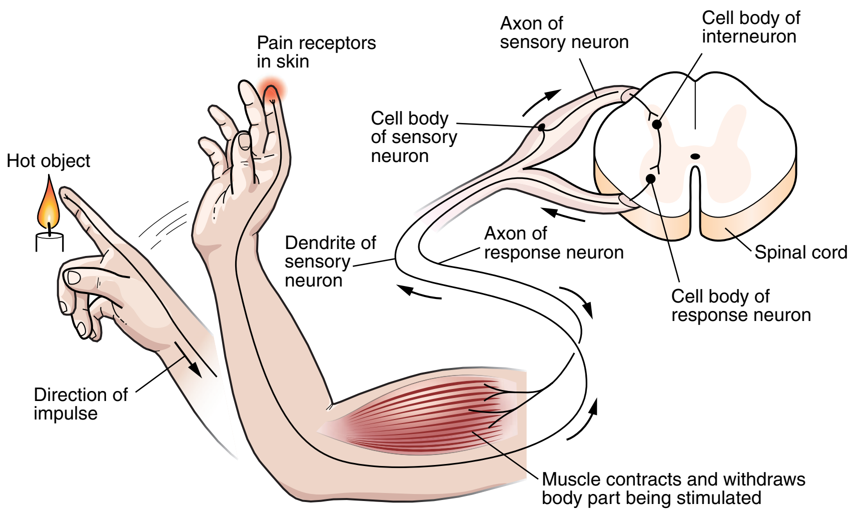

Figure 1.4 A simple spinal motor reflex.

reflexes in the head and **spinal reflexes** in the body. Spinal reflexes consist of both **segmental reflexes**, whose junctions between the stimulus and response neurons are in the spinal cord, and **intersegmental reflexes**, whose junctions are in the brain stem. Throughout the body, reflexes prevent muscles from being stretched too far to cause injury. Reflexes rapidly move body parts out of harm's way, so that touching a hot surface does not result in a severe burn (Figure 1.4), and adjust the tension of muscles in response to changes in the body's center of gravity caused by voluntary movement. This prevents someone from inadvertently toppling over every time one reaches across a counter.

Cranial reflexes in the brainstem again either have protective functions or are components of complex systems. The gag and cough reflexes help clear the throat of noxious substances. A variety of blink reflexes lower the eyelid to protect the eye from harm. As the result of distinct reflexes, people blink in response to a tap on the forehead, a mild shock to the wrist, an intense sound, a flash of light and pressure on the cornea by a touch or puff of air (Aramideh and Ongerboer de Visser, 2002). Three brainstem reflexes, the pupillary reflex, the accommodation reflex, and the vestibulo-ocular reflex, make vision possible. When you go from a dark room to a light one or from a light room to a dark one, the small holes in the surface of each eye called **pupils** reflexively respond to the change in light and close or open just enough to maintain the same amount of light falling on the retina. When you focus on something, muscles contract and relax to change the shape of the eyeball so that a clear image continues to fall on the retina. When you turn your head while you are looking at something, muscles contract and relax so that your eyes roll in the exact opposite direction to maintain a clear image at your fixation point (Figure 1.5).

Collections of segmental reflexes in the brainstem are organized by the superior colliculus and inferior colliculus in the midbrain as **supersegmental** functional systems that orient the body towards visual and auditory stimuli, so you automatically turn towards a bright flash or loud noise. In addition, the eyes automatically fixate on a moving target (Gnadt *et al.*, 1997). These automatic responses are part of an **orientation reaction** that directs perceptual

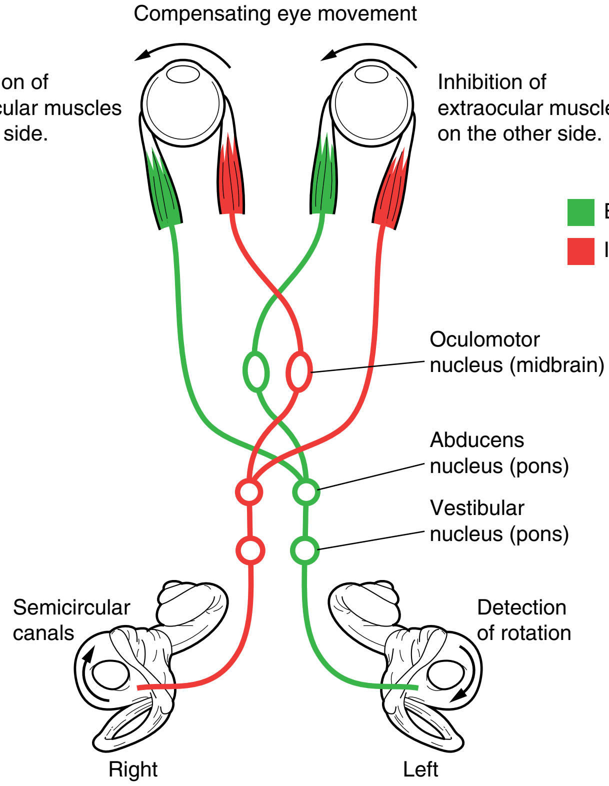

Figure 1.5 The vestibular-ocular reflex is initiated by the vestibular nucleus in the pons of the brain stem. The eyes move in response to changes in the fluid levels of the semicircular canals of the ear, which change as the result of head movement.

processing to a novel input. As shown in **Figure 1.6**, above the midbrain are three structures that further organize reflexes into functional systems. First, the hypothalamus regulates **cranial** and **spinal** reflexes related to eating. The hypothalamus sensitizes salivation and stomach contraction reflexes when a hungry animal is about to eat. Second, the cerebellum modulates cranial withdrawal reflexes, such as the blink reflex and spinal reflexes that stabilize the body in different postures and during locomotion. To coordinate body movements, the **vestibular** system keeps track of the orientation of the body, and this information is used by the cerebellum in making both reflexive and voluntary movements. As you move about you agitate the fluid in the semicircular canals in your ears. The movement of the fluid signals the tilt of your body and activates compensatory vestibular reflexes in the brainstem that keep you from falling (**Figure 1.5**).

Third, the amygdala aggregates and modulates responses of the superior colliculus and inferior colliculus into a comprehensive orienting or startle response that categorizes the stimuli as good or bad and orients the body towards or away from it and prepares the body for action in response to it. Finally, as shown in **Figure 1.6**, the amygdala, cerebellum, hypothalamus, superior colliculus, and inferior colliculus receive inputs from the areas in the frontal, parietal, and occipital cortex that modulate their supersegmental responses so that they support rather than conflict with voluntary movements that are part of the same

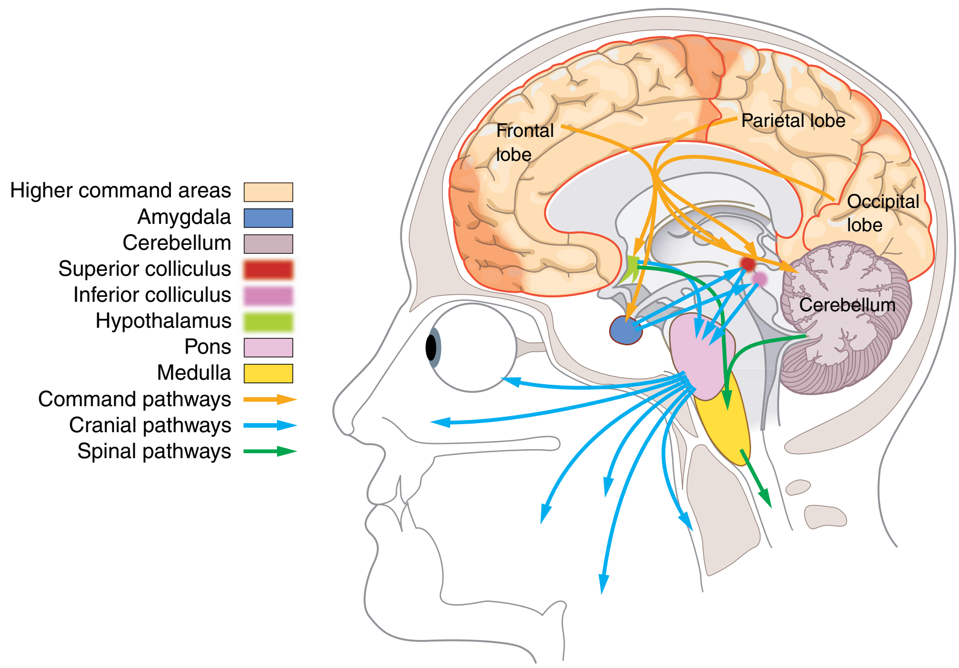

Figure 1.6 Functional systems of reflexes include: the hypothalamus regulates reflexes related to eating; the cerebellum modulates reflexes that stabilize the body; and the amygdala aggregates responses by the superior and inferior colliculus into the orienting response (after an original) figure by Nicole Owen).

functional response. For example, the reflexes controlled by the superior colliculus are part of the visual scanning system that makes visual perception possible (Chapter 3).

The automatic reflexes play important, though secondary, roles in the regulation of voluntary action. A reflex provides an innate fast response to a single, simple, stimulus. A reflex can be fast because it involves only a few sensory neurons and interneurons, so very little processing takes place and there is only a short time before the response is activated. The reflex always occurs without any conscious decision to perform the action. Speed is an advantage. A hand pulls away from a burning stimulus before the person even feels the pain. But simplicity is a limitation. There are no reflexes to things that must be recognized. Recognition requires many computations, so is not simple. Some reflexes have no purpose at all in humans but are vestiges of reflexes that were useful to an ancestor. When a hairy animal is cold, neurons sensitive to the cold activate motor neurons that cause the skin to pucker up, which causes little air pockets close to the skin that are surrounded by hair. This has exactly the same effect as putting on a sweater. The pockets of air are warmed by the animal's body heat and, in turn, help keep the animal warm. In humans, the puckering in the skin is called goose bumps. Goose bumps have no function but remind us that we evolved from creatures whose bodies were covered by hair. In addition, touching the cornea elicits a slight movement of the skin over the jaw. It is not known why this response evolved.

Reflexes are encoded into the nervous system at birth. They are innate. However, innate does not mean permanent. Some reflexes that are present at birth disappear as the infant