Neurology of Learning: An Understanding of Neurology as the Basis of Learning and Behavior in the Domestic Dog

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**Introduction**

The plasticity of the dog’s neurological system provides an ideal medium for learning. Neurology is the basis on which the principles of learning are defined. Aspects of learning principles, such as attention, contiguity (close proximity in time), reinforcement (a consequence that strengthens the behavior), repetition and association have their bases in the neurological structures that consolidate, store and retrieve learning as memory.

The effect of stimulation, in the form of experience, is of particular importance to neurological development during the dog’s critical development periods. Stimulation causes neural activity, resulting in neural growth. Neural systems that are not stimulated during development periods atrophy and die, or otherwise fail to develop normally.

A fundamental understanding of the dog’s neurological system provides first principles on which to construct effective socialization and training plans, and to adjust these plans as the results of learning are observed.

**Learning Principles**

Learning is a process by which experience leads to long-lasting changes in behavior. The predictive mechanisms of the brain help determine what the dog will attend to, and therefore what the dog will perceive and respond to (Ratey, 2001, p. 350).

The natural environment is in constant change. Some changes are cyclic and predictable, such as day and night. Other changes are sudden and unpredictable, such as unusual weather patterns that cause changes in food availability. As an adaptive mechanism, the ability to learn allows an animal to adjust to predictable and unpredictable circumstances that occur during its lifetime (Siiter, 1999, p. 107). Learning provides behavioral plasticity that provides an animal with the flexibility to cope with an ever-changing environment (Domjan, 2003, p. 252).

Some behaviors, such as the nuzzling instinct in newborn pups, are *innate*; they occur without any history of learning and are intrinsically reinforcing (Coppinger & Coppinger, 2001, p. 202). Although such behaviors are under the control of neural programs that are primarily genetically wired, they can become more refined through learning, and may even fail to form if the environment does not provide relevant learning experiences during the critical development period for that skill (Coppinger & Coppinger, 2001, p. 118; Roberts, 1998, pp. 268–269). For example, a young predator may have instinctive hunting skills (track, stalk, chase, kill) but these skills are refined through practice.

The most common methods for behavioral change used in dog training are respondent conditioning and operant conditioning (Roberts, 1998, p. 126). Both of these are based on associative learning processes: the joining of combinations of stimuli and/or responses in space and time (Roberts, 1998, p. 121).

**Respondent Conditioning**

Respondent behavior is reflexive, based on innate or previously learned behavior, which is elicited by a stimulus (Roberts, 1998, p. 135). *Respondent conditioning* results from the pairing of a conditioned stimulus (CS) with an unconditioned stimulus (US), so that the CS...
elicits the same response as the US (Domjan, 2003, p. 66).

Once a CS has been conditioned to predict something the dog wants, such as a morsel of food, it can be used to act as a secondary reinforcer for operant behavior (Roberts, 1998, p. 134). A secondary reinforcer is a stimulus that has been conditioned so that the dog expects a primary reinforcer (something innately reinforcing for the dog) to follow. An example of a secondary reinforcer in dog training is the clicker, a small plastic device that creates a clicking sound when pressed. A clicker can be conditioned as a secondary reinforcer by clicking, and then presenting a small piece of food within half a second of the click. The dog will anticipate food upon hearing the click and is likely to orient to the handler …and, of course, salivate in preparation for food. Once conditioned, the clicker can be used as a secondary reinforcer, to mark behaviors when they occur.

A conditioned emotional response (CER) can be created by associating an object (place, person, etc.) with something that elicits emotion, such as joy, fear, anger or anxiety. The presentation of that object then elicits that emotion (O’Heare, 2007, p. 229).

Factors that affect the success of respondent conditioning include novelty (newness) and salience (relevancy to the dog) of the CS, salience of the US, contiguity of CS–US presentation, context of the training environment and biological preparedness (innate behavior resulting from genetic factors).

**Operant Conditioning**

Operant behavior is goal-directed behavior through the use of skeletal muscles (O’Heare, 2007, p. 235, p. 254). Operant behavior is emitted; the animal chooses to perform the behavior (Roberts, 1998, p. 135). Reinforcement is contingent upon a specific response to a specific stimulus, called a discriminative stimulus (Domjan, 2003, p. 149).

In operant conditioning, the frequency or magnitude of a behavior is either increased or decreased through consequences such as positive reinforcement, no reinforcement, or punishment. Operant learning is measured as an increase or decrease in the probability, latency (time lag between the stimulus and response), speed and strength of response to the discriminative stimulus (Roberts, 1998, p. 135).

Specific discriminative stimuli and specific types of reinforcers may either support or interfere with operant conditioning by eliciting species-specific innate behaviors (O’Heare, 2007, p. 254). For example, use of food to reinforce nose-touch to a target may elicit licking or mouthing instead of nose-touch of the target.

Stimulus control is achieved when the dog can discriminate between two stimuli and respond appropriately (Roberts, 1998, p. 143). For example, the “sit” behavior is under stimulus control when the dog responds to a “sit” hand signal given in a consistent manner by the trainer. Stimulus generalization occurs when the dog responds appropriately to a stimulus that has been altered (Roberts, 1998, p. 142). For example, a visual generalization is learned when the dog responds to a “sit” hand signal given by various people, where the aspects of the cue (speed, arch of the arm, shape and position of the hand, etc.) vary.

Operant conditioning works for dogs because they are motivated to maximize positive outcomes and minimize aversive outcomes. Dogs are constantly performing behaviors, so reinforcing the behaviors we like will cause dogs to choose to repeat those behaviors. Because operant conditioning teaches the dog he can control the environment through his actions, learning itself becomes intrinsically reinforcing (Lindsay, 2000, p. 247).

In dog training, operant conditioning can be used to (Domjan, 2003, p. 137):

- increase the likelihood of a behavior in response to a specific stimulus (or cue), and therefore produce dependability of response
- produce uniformity of response
• encourage variation of response, or creativity of response, toward shaping new behaviors.

Operant conditioning is based on the *three-term contingency*: associations between the antecedents, behavior and consequences (O’Heare, 2007, p. 235). Because the dog is learning these associations during operant conditioning, respondent conditioning is also taking place (Domjan, 2003, p. 192).

Factors that affect the success of operant conditioning include novelty and salience of the discriminative stimulus, contiguity of response and reinforcement, and salience of the reinforcer. Edward Thorndike’s principles of learning apply to operant conditioning. These include (Craighead & Nemeroff, 2002; Thorndike, 1911; “Principles of learning,” n.d.):

- **Readiness** — Is the dog physically and psychologically prepared to learn the behavior?
- **Exercise** — Has the dog practiced the behavior?
- **Effect** — Does the outcome reinforce the behavior?
- **Primacy** — Did the dog perform the behavior the first time he encountered the stimulus?
- **Intensity** — Emotion facilitates learning, as long as it focuses attention but does not distract the dog from the associations to be learned. Did the stimulus and behavior reinforcer evoke emotion? Was it sharp, clear, vivid, dramatic, and/or exciting to the dog?
- **Recency** — Has the behavior been practiced recently?

**Memory**

Goal-directed behavior involves perception, memory retrieval and comparison, the ability to process and predict the consequences of a response to a particular stimulus in a particular context, and motor skill. All of these processes require memory.

In a theoretical model, there are two basic types of memory. *Long-term memory* is information stored either innately or from previous learning. *Working memory* is the combination of information retrieved from long-term memory and environmental information (both internal and external) acquired through the senses (Roberts, 1998, p. 16).

![Figure 1: A model of memory flow](image)

Goal-directed behavior involves perception of the current environment, acquisition of memories from prior similar events, feedback from emotional systems, an understanding of...
oneself in space, the ability to move oneself in a way that will avoid unwanted events and obtain wanted events (behavior), and storage of memories for reference in future similar events (LeDoux, 2002, p. 265; Rodrigues, Schefe, & LeDoux, 2004, p. 80). Working memory allows the dog to bring all this together.

Working memory is processed in the frontal lobes, and is used in registering current activity while retrieving and holding information stored in long-term memory (Ratey, 2001, p. 194, p. 309). Working memory is only temporary. Thoughts in working memory disappear in a short time. To be recalled, they must have been consolidated and stored in long-term memory (Rodrigues et al., 2004, p. 81).

Thorndike’s principles of learning apply to working memory and long-term memory. For example, an event can be stored in long-term memory if it is highly salient to the learner, particularly if emotions are involved (“intensity”). Also, most long-term memory requires repetition (“exercise”) (Rodrigues et al., 2004, p. 81).

Not all memories are stored long term. Interference with working memory disrupts its transition to long-term memory (Rodrigues et al., 2004, p. 81). For example, teaching a dog several new behaviors in one training session can cause interference in one behavior by another behavior (Roberts, 1998, p. 64). Simple or similar tasks are not as prone to interference as complex or disparate tasks (Roberts, 1998, p. 84). Because of this, the best training plans (except for very simple tasks) may be those that teach only one new behavior, allowing the dog time between training sessions for learning consolidation before teaching a second new behavior.

The Neurological System

Learning and behavior are functions of the neurological system, which is comprised of the central nervous system (CNS) and peripheral nervous system (PNS). The CNS consists of the brain and spinal cord. The PNS consists of nerves located outside the brain and spinal cord (Norden, 2007, Part 1, p. 19).

All mammalian neurological systems are similar, with minor differences that help the animal specialize for survival in its particular niche. For example, a human brain has a larger cortex and areas specialized for language and speech, whereas a canine brain has a larger olfactory bulb and more olfactory receptors specialized for processing scent (LeDoux, 2002, p. 303; Lindsay, 2000, p. 79). The continuity hypothesis suggests that psychological and behavioral continuity exists across mammalian species, due to similar neurological system physiology (Roberts, 1998, p. 4, p. 15).

The Functions of Basic Brain Structures

The brain is separated into two hemispheres, right and left (Norden, 2007, Part 1, p. 19). The motor cortex in the left hemisphere is connected to, and therefore controls, nerves routed to the right side of the body, and the motor cortex in the right hemisphere controls the left side of the body (Norden, 2007, Part 1, p. 61). These hemispheres are connected by a bundle of neurons, a commissural pathway, called the corpus callosum, which allows for coordination of thought and movement (Norden, 2007, Part 1, p. 50).

For the purpose of understanding basic evolution, the brain can be subdivided into three areas: the hindbrain, midbrain, and forebrain (LeDoux, 2002, p. 35; Norden, 2007, Part 1, p. 21).

- The hindbrain and midbrain are evolutionarily older, more primitive areas of the brain. Components within these areas support basic functions necessary for life. For example, the reticular formation supports heart rate, breathing, sleep/wake cycles and attention, and the rostral colliculus supports visual reflexes, such as reflexive lunging in response to sudden, fast movement across the dog’s visual field (Norden, 2007, Part 1, p. 21, p. 29, p. 50; Part 3, p. 55).
- The forebrain is the most recently evolved area of the brain, and supports complex behavior such as thinking and problem solving (LeDoux, 2002, p. 35; Norden, 2007, Part 1, p. 21).
The brain is composed of hundreds of functionally distinct, interdependent components (Norden, 2007, Part 1, p. 49, p. 53). This article covers only the most prominent and well-studied structures critical to learning and behavior.

The cortex, amygdala and hippocampus are three particularly important brain regions involved in learning and behavior (LeDoux, 2002, p. 295).

• The cerebral cortex is a large area of the brain, the majority of which is involved in the processing of sensory information (Norden, 2007, Part 1, p. 81). The cortex is divided into four lobes (O’Heare, 2007, p. 103). The frontal lobe supports planning, calculating and understanding consequences (Norden, 2007, Part 1, p. 66; O’Heare, 2007, p. 103; Ratey, 2001, p. 148). The occipital lobe processes visual information, the temporal lobe processes auditory information, and the parietal lobe processes other sensory information (O’Heare, 2007, p. 103). Parts of the frontal and temporal lobes are also involved in emotion and memory (Norden, 2007, Part 1, p. 66). Two areas of the frontal lobe, the prefrontal cortex and orbitofrontal cortex, are involved in impulse control (O’Heare, 2007, p. 103). Working memory is predominantly handled by the prefrontal cortex (Norden, 2007, Part 3, p. 25). The basal ganglia, located in the forebrain, are involved in the extrapyramidal motor system, which processes habitual movement (Norden, 2007, Part 2, p. 179; Part 3, p. 26).

Figure 2: Lobes of the cerebral cortex

• The amygdala is a small, almond-shaped structure. It is acted on by various neurotransmitters and hormones, and has a role in regulating autonomic, endocrine, somatosensory, reproductive, memory, sleep, orientation and other functions (Ratey, 2001, pp. 311–312). The amygdala plays a central role in the expression of fear, aggression and other emotional behaviors (Norden, 2007, Part 2, p. 123). In dogs, the amygdala has been associated with predatory and social behaviors (O’Heare, 2007, p. 102).

• The hippocampus, connected to the amygdala through neural circuits, is activated for storing memory, including peripheral components of memory such as temporal and environmental contexts related to events (Domjan, 2003, p. 285). The hippocampus also processes spatial memory (LeDoux, 2002, p. 114). It functions as a convergence zone, where memories stored in various areas of the brain converge into working memory (LeDoux, 2002, p. 318). Neurons in the hippocampus can be generated throughout life (Nicholls, Martin, Wallace, & Fuchs, 2001, p. 494).
Other components of the brain are also important for learning and behavior.

- The **cingulate gyrus** is a ring of gray matter above the corpus callosum, which projects from the cortex to the hippocampus. It integrates other parts of the brain, and plays a role in social motivation, emotion and movement (Ratey, 2001, pp. 318–319).
- The **thalamus** is a sensory filter that is connected to the *anterior cingulate gyrus* (Ratey, 2001, p. 318). The thalamus coordinates sensory and emotional inputs, and is a gateway to the cerebral cortex, the part of the brain involved in cognitive functions, such as problem solving.
- The **hypothalamus**, located below the thalamus, is part of the hypothalamic–pituitary–adrenal (HPA) system. This system regulates the sympathetic (fight or flight) and parasympathetic (rest and relaxation) systems (Norden, 2007, Part 2, p. 123; O’Heare, 2007, p. 102). The hypothalamus also regulates the body, maintaining homeostasis. For example, thirst and appetite are driven by the hypothalamus, acting to keep the body hydrated and fed (Norden, 2007, Part 1, p. 29, p. 49).
- The **cerebellum** is located at the base of the brain, at the rear of the brainstem. The cerebellum is essential for learning and behavior because it is responsible for coordination of learned-skilled motor movement, as well as cognitive, spatial and memory functions (Norden, 2007, Part 1, p. 30; Ratey, 2001, p. 148).
- The **pons**, located in front of the cerebellum, is the gateway between the cerebellum and the rest of the brain. Motor movement is initiated in the cortex, then travels through the pons to the cerebellum, which coordinates the movement by sending signals down the nerves in the spinal cord connected to the appropriate muscles (Norden, 2007, Part 1, pp. 30–31).
- The **ventral tegmental area** (VTA) is a set of neurons in the midbrain that are involved in the endogenous reward system (Norden, 2007, Part 2, p. 123).
Neurons and Synapses

The neurological system consists primarily of elongated cells called neurons. There are approximately 150 different types of neuron, making it the most diverse type of cell in the body (Norden, 2007, Part 1, p. 35).

The general description of a neuron is as follows, although different types of neuron vary according to their function. The core of the neuron is the cell body, or soma. This is similar to the soma of other cells. Sprouting from the soma are branching fibers called dendrites. From these branches bud small protuberances called dendritic spines. Exiting from one end of the soma is an elongated projection called an axon. A ridge between the cell body and the axon, called the axon hillock, controls impulses flowing from the dendrites down the axon. The axon is covered with an insulating material called a myelin sheath, which facilitates fast transmission of nerve impulses.

Neurons obtain structural support from glial cells, the majority of cells that compose the brain. Glial cells also produce myelin sheathing, form the blood–brain barrier that is vital to brain function, and absorb and dispose of cellular debris (Lindsay, 2000, p. 75).

The axon of one neuron meets the dendrites of other neurons, without actually touching. This space between the axon and dendrites is called the synaptic cleft, or synapse (Kalat, 2004, pp. 32–36). Neurons communicate by sending electrochemical signals, which run down the axon and across the synapse to adjoining neurons (LeDoux, 2002, p. 41). These messages excite or inhibit adjoining neurons (O’Heare, 2007, p. 105).
One neuron can have numerous axons and dendrites. This allows messages to be sent by one neuron and received by many, or sent by many neurons and received by one (LeDoux, 2002, p. 42). This convergence is necessary for consolidation of information from various senses, and to synchronize memory and movement (LeDoux, 2002, pp. 315–318).

Neurons network with other neurons in the brain and spinal cord, as well as various sensory receptors (gustatory, somatosensory, olfactory, visual and auditory) throughout the body. Messages coming to the brain from the body use the afferent system. Messages traveling from the brain to the body use the efferent system (O’Heare, 2007, p. 105).

There are trillions of synaptic connections in a mature mammalian brain (Norden, 2007, Part 1, p. 111). Groups of neurons that are linked together form a circuit. This allows a given neuron to support more than one function (Ratey, 2001, p. 167). Complex circuits form functional systems, which perform specific functions such as seeing or hearing (LeDoux, 2002, p. 49).

There are two categories of neuron involved in messaging: interneurons and projection neurons. Interneurons send messages within their local circuit, and can be excitatory or inhibitory. Projection neurons make up projection pathways, which send excitatory messages to other circuits (LeDoux, 2002, pp. 49–50; Norden, 2007, Part 1, p. 61). Projection pathways synchronize separate areas of the brain, allowing the system to function as one (LeDoux, 2002, p. 61). For example, various areas of the cortex are connected by bundles of axons called association pathways (Norden, 2007, Part 1, p. 59).

Synaptic connections between neurons give the brain an ability to change in response to the environment (LeDoux, 2002, p. 9). This plasticity forms the foundation of learning and behavior (Norden, 2007, Part 3, pp. 23–25).

Patterns of activity in the brain cause synapses to be formed, strengthened or weakened (Nicholls et al., 2001, p. 480). These patterns of activity result from internal stimuli, such as sensations the dog has of his body moving through space, and external stimuli, such as olfactory or visual stimulation (LeDoux, 2002, p. 3). In a literal sense, experience changes the brain.

Although the majority of learning involves the brain, simple forms of learning can occur in the neural tissue that lies below the brain (Domjan, 2003, p. 156). In addition, some responses (particularly reflexive responses) occur without the involvement of the brain (Ratey, 2001, p. 156).
Neurotransmitters and Hormones

Processes in the neurological system are mediated by hormones and neurotransmitters, a complex mix of chemicals that affect learning and behavior. These chemicals are synthesized from other chemicals, which are either produced by the body or obtained through the dog’s diet (O’Heare, 2007, p. 105).

Neurotransmitters facilitate message transmission between neurons. **Glutamate** and **gamma-aminobutyric acid (GABA)** are the two major neurotransmitters in the mammalian brain (Norden, 2007, Part 1, p. 137).

- **Glutamate** is an amino acid, used by the brain for many functions. For example, it acts as a building block for peptides and proteins, helps detoxify the brain of ammonia, and elicits firing in a postsynaptic neuron (LeDoux, 2002, p. 53). Glutamate is an excitatory neurotransmitter.

- **GABA** is an inhibitory neurotransmitter. Unchecked excitation can damage or destroy neurons. To counterbalance excitation, inhibitory neurons release the neurotransmitter GABA, which decreases the firing in postsynaptic cells, thereby resetting the circuits (Norden, 2007, Part 1, p. 137). This balance of excitation and inhibition provides a means of directing brain activity (LeDoux, 2002, pp. 50–53).

Not all results of excitation involve excitation of the system. For example, serotonin excites GABA inhibitory cells in the amygdala, which inhibit amygdala projection cells, resulting in inhibition (LeDoux, 2002, p. 315). Serotonin can, therefore, have a calming effect. In addition, a neurotransmitter can be excitatory or inhibitory depending on the properties of the postsynaptic receptor. For example, dopamine is excitatory at some synapses and inhibitory at others (Norden, 2007, Part 1, p. 138, p. 146).

GABA and glutamate are fast-acting neurotransmitters. Other neurotransmitters, called **modulators**, have a prolonged and widespread action. Modulators prime various areas of the brain, preparing for processing across multiple senses and various areas of the brain. This facilitates an event that affects multiple stimuli to be understood and learned as one experience (LeDoux, 2002, p. 313).

Modulators include **peptides**, **monoamines** and **hormones**.

- Peptides include **endorphins** and **enkephalins**. Endorphins and enkephalins are triggered by pain and stress, and act as natural painkillers.

- Monoamines include **serotonin**, **dopamine**, **epinephrine** and **norepinephrine**. Some monoamines, such as epinephrine, can facilitate arousal, while others, such as serotonin, can reduce anxiety and increase impulse control (O’Heare, 2007, pp. 105–108). The monoamine acetylcholine is required for muscle movement, including heart and lung function (LeDoux, 2002, pp. 56–59). Dopamine is called the “learning neurotransmitter” because it depolarizes neurons, preparing them to fire. Dopamine is required for motor coordination, attention and the experience of reward (O’Heare, 2007, pp. 105; Ratey, 2001, pp. 120–123). Dopamine is also involved in the experience of pleasure and in addictive behavior (Norden, 2007, Part 1, p. 149; O’Heare, 2007, p. 105). Too much dopamine activity can lead to impulsivity or irritability (O’Heare, 2007, p. 117).

- **Hormones** include **cortisol**, **oxytocin**, **estrogen** and **testosterone**. Hormones are excreted into the bloodstream by the **endocrine system** and act on target organs (O’Heare, 2007, p. 107). Hormones also affect memory and emotion (LeDoux, 2002, p. 60). For example, oxytocin is a peptide hormone released by the hypothalamus that plays a role in social bonding (Norden, 2007, Part 2, p. 137).

Different dog breeds, and different individuals within a breed, have differing amounts of the various neurotransmitters in their neurological systems, and slightly differing brain structures. This can account for varying temperaments and activity levels in their
behavior (Coppinger & Coppinger, 2001, p. 197).

**The Making of Memories**

Categories of information and motor activity are stored across various neural circuits. This redundancy mitigates risk of memory loss; if a few cells in the circuit die, the remaining cells carry on the work. This is referred to as *equipotentiality* (MacLean, 1949, cited in LeDoux, 2002, p. 99).

The excitation and inhibition of neural circuits constitute the encoding of associations, emotion and muscle movement into learning, memory and behavior (Domjan, 2003, p. 68; Norden, 2007, Part 1, p. 135). Each time a behavior occurs, neural circuits organize themselves to better support that behavior by changing their connective patterns (Ratey, 2001, p. 11).

**Action Potentials**

Neurons either fire or they don’t fire. The activation of a particular firing pattern can inhibit or excite other firing patterns, leading to complex learning and behavior (Ratey, 2001, p. 195). Neurons that become more positively charged are *depolarized*, leading to *excitation*. Neurons that become more negatively charged are *hyperpolarized*, leading to *inhibition* (Norden, 2007, Part 1, p. 126).

Ions such as sodium (Na\(^+\)), potassium (K\(^+\)) and chloride (Cl\(^-\)) are distributed in the neuron in a way that makes the inside of the cell more negatively charged than the outside. This creates the neuron’s *resting potential*. This ionic balance is important for maintaining neuron health (Norden, 2007, Part 1, p. 124).

Stimulation of the neuron causes the inside of the cell to change (Norden, 2007, Part 1, p. 138). When glutamate binds to a neuron’s postsynaptic receptor, a passage opens in the receptor that allows positively charged ions to move inside the neuron. This changes the chemical balance between the inside and outside of the cell (LeDoux, 2002, p. 55). When a neuron is stimulated to a level that crosses the axon hillock, it generates an electrical signal that travels down the axon. This is called an *action potential* (Norden, 2007, Part 1, p. 123).

The action potential produces an influx of calcium (Ca\(^{2+}\)) that causes vesicles in the presynaptic terminal to fuse with the cell membrane. This triggers vesicles of neurotransmitter to be released from the presynaptic terminal (Norden, 2007, Part 1, p. 111, p. 124). Neurotransmitter molecules bind with receptors on the postsynaptic membrane. This initiates ionic changes in the postsynaptic terminal. If enough neurotransmitter is taken up by an adjoining neuron, it will result in an action potential in that neuron, and so on. Through this cascade effect, the message travels electrochemically through the neural circuit (Norden, 2007, Part 1, pp. 125–126).

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![Figure 6: Synapse](image-url)
Any neurotransmitters that remain in the cerebral fluid are taken into the presynaptic terminal by transporter molecules and recycled (used again), or destroyed by glial cells. This ensures that excitation does not continue indefinitely (Norden, 2007, Part 1, p. 121).

When GABA binds to a neuron’s receptor, negatively charged ions move inside the neuron. This reduces the effectiveness of the positively charged ions collected as a result of glutamate. When GABA is present, more glutamate is required for an action potential to result (LeDoux, 2002, p. 55). In this way, GABA and glutamate balance electrochemical activity.

**Long-Term Potentiation**

The firing of a neuron is a temporary event. When a stimulus is presented, neural circuits fire in response to that stimulus. Those same circuits continue to fire after the stimulus has gone, preserving the perception of the stimulus in working memory. As time passes, the neurons begin to cease firing, and the thought is lost from working memory (Ratey, 2001, p. 113).

For example, you begin to teach your puppy to sit using a lure. After five repetitions of the behavior, your puppy sits on a hand signal without a lure. An hour later, you cue your puppy to sit using a hand signal, but he doesn’t respond. The association of the “sit” response to the hand-signal stimulus is no longer in working memory, and may not yet be stored in long-term memory. This is because permanent physiological changes need to occur in order for memory to be stored long term. These physiological changes are known as long-term potentiation (LTP).

During an action potential, calcium enters the cell. Enough calcium activates kinases, enzymes that stimulate genes to produce proteins that strengthen the synapse, and also releases neurotrophins, growth chemicals that nourish neurons and cause them to sprout new branches, to form new synaptic connections (LeDoux, 2002, p. 153). As a result, several basic changes occur that increase the firing potential of the neural circuit supporting the memory or behavior (Norden, 2007, Part 3, pp. 28–29; Sapolsky, 2005, pp. 19–23):

- More neurotransmitters are produced in the presynaptic neuron.
- More receptors are created in the postsynaptic neuron, and more dendritic spines sprout, increasing the neuron’s capability of gathering neurotransmitters.
- The postsynaptic neuron increases in width, to better transmit the message downstream.
- More neurons are recruited for the task, and in some cases more neurons are formed.

For working memory, kinases act on proteins that are readily available in the cell (Ratey, 2001, p. 195). However, changes that build long-term memory require a specific protein that is not freely available, and therefore must be synthesized by the cell (Ratey, 2001, p. 195; Rodrigues et al., 2004, p. 81). Specifically, a protein called CREB activates the cell to synthesize other proteins that cause long-term changes to the neuron, further stabilizing the connections (LeDoux, 2002, pp. 149–150; Ratey, 2001, p. 195).

LTP is specific to the synapses involved in the potentiating experience. Therefore, a neuron can participate in the storage of various bits of information, through various synaptic connections with multiple other neurons (LeDoux, 2002, p. 141).

The more often a neural circuit is fired, the more physiological changes occur, and the more permanent the learning becomes (Ratey, 2001, p. 191). This is why repetition is so important for learning.

**Storage and Retrieval of Long-Term Memory**

Memory consolidation occurs during sleep (LeDoux, 2002, p. 107). The neural circuits in the hippocampus that fire during learning of a specific new behavior also fire during the period of sleep that follows the learning. It appears that a period of sleep called rapid-eye-movement
(REM) sleep assists in the formation of long-term memory (Ratey, 2001, p. 188).

Memory, particularly of complex behavior, is initially stored as synaptic changes in the hippocampus and frontal cortex. Each time the stimulus is repeated, the memory is reinstated in the cortex, and the neural circuits supporting the memory grow stronger. Multiple reinstatements of the memory cause synaptic changes in the cortex. In addition, behaviors that are practiced to proficiency, particularly simple motor behaviors, begin to be processed lower in the brain, in the basal ganglia, brainstem and cerebellum (Ratey, 2001, p. 158). As the work is taken over by the cortex and lower areas of the brain, the hippocampus is freed for other processing (LeDoux, 2002, p. 107).

Because encoded memory is distributed across various neural circuits, it needs to be mapped to be retrieved. Neural circuits are mapped by various areas of the brain, such as the hippocampus, cerebellum, and basal ganglia (Ratey, 2001, pp. 142–143).

Once retrieved, memories of various aspects of an event need to be amalgamated. For example, memory of scent may be retrieved from one area of the brain, and memory of sound from another area. The hippocampus is involved in retrieval and consolidation of memories (Ratey, 2001, pp. 185–186, p. 194).

**Functional Systems of Behavior**

Many different functions are required to sustain life. Each function is supported by specific systems of behavior, which consist of interconnected neurological components (Norden, 2007, Part 1, p. 49). These systems provide the animal with a means to find and consume food, seek mates, or detect and avoid danger (LeDoux, 2002, p. 303). A few of the most vital systems involved in learning are the attention system, perception systems, the motor system and the limbic system.

**The Attention System**

At any given moment, a dog’s perceptual systems are receiving a multitude of various inputs. It would be impossible for the dog’s memory systems to process and store all of these inputs. Attention is the serial process by which the dog attends to only one input at any given moment, allowing processing and response to that input (Roberts, 1998, p. 28, p. 34).

Attention is required for learning to occur (Ratey, 2001, p. 123). Attention is given when a stimulus is surprising or relevant to the dog in that environment at that time. Attention is a serial process; if a dog’s attention is divided, he will find learning more difficult (Roberts, 1998, p. 52, p. 62).

The attention process is comprised of (Ratey, 2001, pp. 115–120):

- **Arousal:** The animal becomes more alert. This is controlled by the reticular activating system, connecting the frontal lobes, limbic system, brainstem and sense organs.
- **Orientation:** The animal involuntarily orients to, and focuses on, the stimulus. This involves various brain components. For example, the posterior parietal cortex helps the animal to disengage from other stimuli. The basal ganglia and frontal parietal attention circuits help the animal shift the focus of attention to the new stimulus. Neurons in the thalamus inhibit other distractions.
- **Novelty detection:** The hippocampus compares the stimulus with stored memories to check its novelty. A stimulus or outcome that is novel, or otherwise triggers an emotional reaction such as surprise or excitement, will cause the hippocampus to store the memory (Lindsay, 2000, p. 238).
- **Assessment:** The frontal lobe uses the comparison to identify an appropriate response, and allows the animal to sustain attention. In the temporal lobes, the caudate nuclei and basal ganglia act to filter out background “noise,” both internal and external, so that attention can be maintained. Meantime, the anterior cingulate gyrus helps coordinate the attention system and allows the animal to distribute attention when needed.
Attention is required for learning. Because of this, new learning is more easily introduced in a familiar environment, so the animal is not distracted by novel environmental stimuli (Lindsay, 2000, p. 209).

A novel stimulus attracts attention, leading to a stronger association (Roberts, 1998, p. 156). Once the stimulus is no longer novel, the association is less likely to be learned. Because of this, the first memory of a novel stimulus–stimulus or stimulus–response association is the strongest. This is referred to as first-order learning. First-order learning parallels Thorndike’s “primacy” principle of learning.

If two stimuli are presented simultaneously, attention will be given to the stimulus of most interest, and association with that stimulus is likely to be learned. The more salient stimulus competes for attention with the other stimulus, so the association with the second stimulus is less likely to be learned. This is called overshadowing (Roberts, 1998, p. 146). For example, if a dog is taught to sit using a hand signal and the word “sit” simultaneously, the dog will likely learn the hand signal cue but not the word cue. This is because body postures are more relevant to dogs than language, so the hand signal will overshadow the verbal cue. To avoid overshadowing, one cue should be taught at a time.

If a verbal cue has already been learned, and the hand signal is given at the same time as the verbal cue, the hand signal will not be easily learned due to an effect called blocking. Attention to the previously learned cue blocks the learning of the new cue (Roberts, 1998, p. 147). To avoid blocking, the new cue should be given first, then the old cue. This allows the dog to pay attention to both the new and old cues, and begin to anticipate the old cue when the new cue is presented, leading to learning of the association between the new cue and the behavior.

In dog training, attention is often viewed as “watching”. However, attention does not necessarily require watching. If that was the case, then blind dogs would not be able to learn.

**Perception Systems**

Perception is stimulation of the senses, which causes neural circuits to form and strengthen, leading to learning (Ratey, 2001, pp. 48–109).

Perception is not just the input collected by the senses. It is also the processing of that input by the brain (Ratey, 2001, p. 53). The sensory system provides the dog with a means to obtain input both from within his own body and from the world around him (Norden, 2007, Part 1, p. 172). The brain transforms these inputs into meaningful information and behavior (Lindsay, 2000, p. 74).

Environmental stimuli are received through the sense organs and relayed to the nervous system, where they are analyzed. The eyes do not see; they are receptors that transmit light waves to the brain, which builds a picture based on this transmission, filling in areas where information was not received. The ears do not hear; they transmit sound waves to the brain, which builds sound (Norden, 2007, Part 1, p. 55; Part 2, p. 18). What a dog sees and hears is a result of receptors, innate knowledge, learning history and the current state of his neurological system.

Each of these perceptual systems experiences a different world; a different aspect of a single experience. Working memory binds these perceptions together as one experience (LeDoux, 2002, p. 308).

Sensory capability is different in humans and dogs (Beaver, 1999, p. 43). In order to truly understand why a dog behaves the way he does, you would need to experience the world through his perception systems (Grandin, 2005, pp. 28–67). That is, not just through his eyes or ears, but through the brain components that process these senses.

It is not possible for a human to smell what a dog smells, hear what a dog hears, or see contrast, color and movement the way a dog sees. But we can make an attempt to understand the dog’s senses, view the world from the dog’s
angle, and try to imagine why the dog behaves as he does (Grandin, 2005, pp. 1–67).

**The Somatosensory System**

*Somatosensation* (touch) is the earliest used, and possibly the most important, of all canine senses (Fogle, 1990, p. 26). A puppy’s natural reflex of pushing his head into warm objects helps him keep close to his mother and littermates, and helps him find the source of milk (Beaver, 1999, p. 55). Without a sense of touch, the newborn pup would not survive.

Somatosensation relies on various specialized receptors that include thermoreceptors, chemoreceptors, mechanoreceptors and proprioceptors. These receptors carry information such as heat, itch and pain to the thalamus, which transmits it to the primary somatosensory cortex. This gives the dog information about both external and internal environments (Norden, 2007, Part 2, pp. 32–33).

Thermoreceptors are responsive to heat and cold. Chemoreceptors are responsive to chemical stimulation. Nociceptors are responsive to noxious or painful stimulation (mechanical, chemical or thermal) that may damage body tissue. Nociceptors elicit species-typical escape responses. They relay information through two pathways: the fast pain system and the slow pain system. The fast pain system results in immediate response because it travels directly to response systems in the brain, bypassing the limbic and learning systems. The fast pain system is associated with startle reaction, and is not affected by pain-relieving chemicals such as endorphins. The slow pain system, associated with throbbing or other constant pain sensation, travels through the limbic system, which causes a secretion of pain-relieving chemicals such as endorphins (Lindsay, 2000, pp. 150–152).

Mechanoreceptors are responsive to physical changes, such as pressure or the stretching of skin produced when hairs, such as the dog’s vibrissae, are moved (Lindsay, 2000, pp. 150–151). Unlike humans, the dog has vibrissae (facial whiskers) above his eyes and on the sides of his muzzle. These areas of the skin have a high volume of blood supply and nerve endings, allowing dogs to sense air flow, current, and the shape and texture of objects (Fogle, 1990, p. 27). A disproportionate amount of the cortex is devoted to processing information received through whiskers (Norden, 2007, Part 2, p. 35).

Dogs respond differently to touch depending on socialization, prior learning, general physical condition, and current emotional state (Lindsay, 2000, p. 150). Generally, when a person gently strokes or massages a familiar dog, relaxation occurs. Massage stimulates nerve pathways, lowering levels of stress hormones such as cortisol and epinephrine (Ratey, 2001, p. 363). Tactile stimulation increases the activity of the vagus nerve, a cranial nerve that influences heart rate and food absorption (Ratey, 2001, p. 363). Chemicals such as oxytocin and endorphins are released by the hypothalamus into the pleasure centers of the brain (Norden, 2007, Part 2, pp. 145–146). Oxytocin is a chemical known to facilitate the bonding of mother and child, and endorphins cause a state of euphoria (Ratey, 2001, p. 245, pp. 328–330).

Proprioceptors are responsive to body movement and position. Proprioceptors give the dog a perception of his body’s position and allow him to coordinate movement (Lindsay, 2000, p. 152). The dog receives kinesthetic feedback from these receptors in muscles, tendons and joints (Roberts, 1998, p. 122). This provides fast moment-to-moment information about the body’s movements and its orientation relative to the location of its different parts (Lindsay, 2000, p. 152). Balance is maintained by a combination of proprioceptors that provide information about the body’s orientation in space, and hair-like receptors in the inner ear that bend in various directions when displaced by cochlear fluid when the head changes position. This gives the brain information about the orientation of the head relative to the direction of gravity (Lindsay, 2000, pp. 152–153).

Proprioceptive input stimulates brain cells. If a motor skill is practiced often, it will change the structure of the somatosensory cortex as
neurons are recruited for the task. For example, violin players have additional area in the somatosensory cortex devoted to their fingers (Norden, 2007, Part 3, p. 31).

Physical exercises that stimulate proprioception can teach the dog body awareness. For example, lay a ladder on the ground and lead the dog slowly through it length-wise, on a loose leash or off leash. Or lay a dozen poles on the ground, as for cavaletti, but unevenly spaced and slightly skewed so the dog needs to pick his way through carefully, and send the dog through slowly. The poles can be raised slightly by setting the ends on crushed aluminum cans (Zink, 2006, Part 6).

The Visual System

Because they have evolved to hunt at dusk or dawn, dogs have less need for acute focus and color vision than do humans, and a greater need for low-light and movement vision (Beaver, 1999, p. 46). Otherwise, a dog’s eyes are similar to a human’s.

Light rays pass through the cornea and lens via the pupil. The eye focuses these rays onto the retina, a sheet of neural tissue at the back of the eye. Because the lens is convex, it reverses and inverts the image. But the brain will later correct this image (Norden, 2007, Part 1, p. 167).

The retina is made up of two types of visual receptors: rods and cones. Rods are specialized for low-light conditions, and receive information about contrast and movement. Cones receive information about color and detail. A dog’s eye has fewer cones (color receptors) than a human’s. Therefore, dogs are unable to uniquely identify certain colors in the spectrum that can be identified by the human eye (Beaver, 1999, p. 47; Lindsay, 2000, p. 128).

Because a dog’s retina is comprised predominantly of rods, which are responsible for light collection, it is capable of collecting more light than a human retina. The dog’s eye also contains a reflective surface behind the retina called the tapetum lucidum, which reflects light that enters the eye and causes a greater sensation of light (Beaver, 1999, p. 46; Lindsay, 2000, p. 130). When color differentiation is low and light-gathering capability is high, changes in contrast become more obvious than changes in color (Grandin, 2005, p. 43).

Compared with humans, dogs have poor close vision and reasonably good distance vision (Fogle, 1990, p. 33). Dogs are unable to focus on objects closer than 33–50 cm (Beaver, 1999, p. 46). Several factors affect the dog’s ability to focus. Dogs have fewer cones, which are responsible for depiction of detail (Norden, 2007, Part 1, p. 167). Because a dog’s eye collects more light, the retinal image becomes fuzzier (Beaver, 1999, p. 46). Unlike a human eye, a dog’s eye does not have a macula lutea, which would enhance visual acuity (Beaver, 1999, p. 46). Dogs also have a larger lens-to-globe ratio than humans, making near focus more difficult (Beaver, 1999, p. 46). Functionally, the level of farsightedness in dogs is insignificant for their survival, because it would not affect the dog’s ability to hunt (Beaver, 1999, p. 46).

A dog’s eyes are set more on the sides of the head, less forward-looking, than a human’s eyes. Because of this, a dog has a wider field of view than a human. Depending on the breed, the field of vision is about 240 to 290 degrees for a dog, but only 180 degrees for a human (Beaver, 1999, p. 46). This large field of vision allows the dog to easily scan his surroundings.

Overlap of vision from both eyes, at the front of the face, provides binocular vision and depth of field. Although dogs generally have better binocular vision than prey animals, they have less binocular vision than humans (Lindsay, 2000, pp. 130–131). In most breeds, the eyes are set closer to the sides of the face and less toward the front, providing about 40 to 60 degrees of overlap between the right and left eyes (Lindsay, 2000, pp. 130–131). Therefore, a dog’s binocular vision is limited to a small angle in front of him (Lindsay, 2000, p. 131). In addition, dogs have about half as many uncrossed nerve fibers (needed to support binocular vision) as humans (Beaver, 1999, p. 46).
As predators, dogs are tuned to movement. Having more rods than cones causes the dog’s eyesight to have less visual detail, but an increase in contrast and movement sensitivity, compared with the human eye (Lindsay, 2000, p. 130). A dog’s wide field of vision also makes him more sensitive to peripheral movement (Fogle, 1990, p. 33). This attention to movement may explain why dogs have an “acute sensitivity to movement and subtleties of gesture” and are able to recognize individuals at a distance (Lindsay, 2000, p. 132). Typically, dogs are able to recognize moving objects at 810–900 meters, but stationary objects at only 585 meters (Beaver, 1999, p. 48).

Eyesight does not end with the collection of light. Axons from the retina form the optic nerve and transport information about received light rays to the thalamus. This, in turn, transports visual information to the visual cortex, where the image is processed (Norden, 2007, Part 1, pp. 174–179; Part 2, p. 4, p. 17). Interpretation, including filling in of blank areas, is an important factor in construction of an image in the visual cortex. For example, the spot in the back of the eye where the optic nerve exits has no receptors, so that area of the image is blank. The brain fills in the area based on information received and previously learned (Norden, 2007, Part 1, pp. 174–179; Part 2, p. 4, p. 17). This is why the dog “sees” with his brain, not his eyes.

**The Auditory System**

As with sight, sound is a creation of the brain. Sound waves enter the ear, vibrating the tympanic membrane (ear drum). This vibration is transmitted by a chain of three tiny bones, which focus the energy on the inner ear. The liquid in the inner ear transmits these waves across hair cells, auditory receptors in the inner ear. Auditory neurons increase or decrease their firing in response to this stimulation. The auditory nerve carries messages from the ear to the thalamus, which sends these messages to the primary auditory cortex in the temporal lobe. The auditory cortex interprets sound into meaningful information, such as pitch, tone, intensity and direction (Norden, 2007, Part 2, pp. 19–20).

Dogs can hear sounds in a broadly similar fashion to humans, except that dogs can hear at longer distances, have larger pitch ranges and are better able to locate the sound source. In addition, more of the dog’s brain is devoted to sound than a human’s brain is (Fogle, 1990, p. 31). Dogs can hear with much better source-location accuracy, because the pinna (outer ears) are controlled by muscles that allow the dog to move them individually, scanning the environment and collecting sound from various directions.

Locating sound relies on complex brain calculations based on the minute time differences between the sound waves reaching each of the ears (Lindsay, 2000, p. 134). If the location of a sound is not equidistant from the two ears, it will arrive in the closer ear slightly before the opposite ear. This difference in sound arrival time is in the order of millionths of a second (Lindsay, 2000, p. 134).

Hearing is used to communicate, locate group members, and find prey (Serpell, 1995a, p. 260). An important function of hearing in dogs is the ability to avoid danger. Intensity of sound helps determine the immediacy of danger, so auditory sensors are well connected to the limbic system. The auditory system is connected to the thalamus and cortex. These are connected to the amygdala, which in turn connects with the brainstem areas that control fear responses. When a dog hears a loud or sudden sound, the amygdala determines the intensity of sound through its connection with the thalamus (the quick route), and activates a startle response if appropriate. The slower route, through the cortex, is then engaged to assess appropriate action (LeDoux, 2002, pp. 121–123).

**The Olfactory System**

The sense of smell is an important sense for dogs (Thorne, 1995, p. 107). A dog’s olfactory sense is used for detection of prey animals, social functions such as scent marking, food identification and other, less understood functions, such as scent rubbing (Beaver, 1999,
A dog’s sense of smell is approximately 10,000 times as sensitive as a human’s (Beaver, 1999, p. 52). His sense of smell is so powerful and precise that a dog can detect a variety of substances at concentrations up to one hundred million times lower than humans can perceive (Thorne, 1995, p. 107). This is due to physiological differences in the olfactory perception system.

In dogs, the olfactory epithelium (the surface inside the nasal cavity that contains scent receptor cells) has up to 250 million receptor cells (depending on the breed). In humans, the olfactory epithelium contains only about 5 million receptor cells per nasal cavity (Lindsay, 2000, p. 137). Dogs also produce far more nasal mucus (the medium used to capture scent molecules) than humans (Fogle, 1990, p. 36).

The sniffing action (a disruption to the regular breathing pattern) causes air to be taken into the nostril and passed over a bony structure called the subethmoidal shelf (a structure humans don’t have) on its way to the scent receptors. Air above the subethmoidal shelf is retained when the dog expires air, allowing scent molecules to accumulate. Scent molecules are dissolved in mucus, which sticks to the receptor cells in the olfactory epithelium (Fogle, 1990, p. 36).

Unless the scent is directly in front of the dog’s nostrils, there is a minute time delay (in the order of tenths of a millisecond) between scent molecules entering one nostril and reaching the other nostril, allowing the dog to calculate the general direction of origin of the odor (Lindsay, 2000, p. 143).

The dog’s brain is specialized for olfaction. In humans, the olfactory bulb is about the size of a raisin and is connected to the scent organs through fibers entering from the front. In dogs, the olfactory bulb is about the size of a plum, and is connected to the scent organs through fibers entering from the sides, above and below (Beaver, 1999, p. 52). Neurons in the olfactory bulb can be generated throughout life (Nicholls et al., 2001, p. 494).

Signals from scent molecules are registered by olfactory receptors and travel to the olfactory bulb. These signals travel to the primary olfactory cortex. From there, signals travel to the thalamus, which transmits them to the orbitofrontal cortex for associative processing. The signals also travel directly from the olfactory bulb to the amygdala, hippocampus and other areas of the brain. In this way, scent bypasses higher cognitive function for faster access to centers that process emotion (Lindsay, 2000, p. 79).

Dogs have a second olfactory system called the vomeronasal organ (VNO) (Beaver, 1999, p. 54). The VNO is located in the back of the palate. Ducts flow from the mouth, behind the upper front teeth, into the VNO (Lindsay, 2000, p. 145). Flehman behavior (licking, mouth smacking and tongue flicking) opens the ducts to allow pheromones, particularly those related to sex hormones, to access the VNO (Beaver, 1999, p. 54; Lindsay, 2000, p. 145).

The olfactory system is directly connected to the amygdala, allowing scent to arouse memory and emotion (Ratey, 2001, p. 62, p. 331).

**The Gustatory System**

In dogs, taste is important for food selection and digestion. For an omnivorous animal like the dog, the ability to safely select a variety of foods provides nutrition for survival in times of scarcity (Thorne, 1995, p. 111). Taste also triggers the appropriate digestive juices in the gastrointestinal system (Lindsay, 2000, p. 149). This prepares the dog’s digestive system for action.

Taste for humans and dogs is apparently similar and includes sweet, salty, bitter and sour (Beaver, 1999, pp. 50–51). However, the sense of taste in dogs is not as refined as in humans. Dogs have only 1,706 taste buds, whereas humans have around 9,000 (Fogle, 1990, p. 28).

Taste is functioning at birth and is closely related to the sense of smell; both are chemical
senses (Fogle, 1990, p. 28). Taste preferences are innate, but are also affected by experience, including prenatal experience. Amniotic fluid and the milk from a lactating bitch may contain food flavors that affect early food preferences (Thorne, 1995, p. 109). If a dog is not exposed to novel foods early in life, he may develop preferences for familiar foods and avoid novel foods (Fogle, 1990, pp. 28–29; Lindsay, 2000, p. 148).

Taste is mediated by an area of the hindbrain called the nucleus of the solitary tract, which connects with neurons from the taste buds spread across the tongue, and nerves from the gut that report on the state of the stomach and intestines, such as nausea. Taste buds are washed with a coating of saliva that brings the taste receptors to baseline (no firing, so no taste). When a tastant is mixed with saliva, it can either excite or inhibit taste receptors, and a taste sensation is generated (Lindsay, 2000, p. 146). Information from the taste buds is transmitted through cranial nerves to specific areas of the brain. Many of these pathways go to cortical areas responsible for the conscious experience of taste.

One specific pathway, which carries information to the amygdala (a part of the emotion-processing system in the brain), may be responsible for taste aversion (Lindsay, 2000, p. 146). Taste aversion is an unusual conditioned response, in that the association can occur even if nausea is experienced much later (hours rather than seconds) after the stimulus is experienced (LeDoux, 2002, p. 127). Pairing of taste with nausea, and detecting novel tastes, are likely the function of several areas, including the thalamus, amygdala and taste areas of the cortex. These are connected by projection neurons to an area of the midbrain called the parabrachial nucleus, to which the solitary tract projects neurons (LeDoux, 2002, p. 128).

The Motor System

Movement is central to behavior because it allows the dog to act on the world around him (Norden, 2007, Part 2, p. 126; Ratey, 2001, p. 148). The motor system, which controls movement, can be divided into three subsystems (Norden, 2007, Part 2, pp. 62–63):

- The pyramidal motor system primarily initiates motor movement. Neurons in the motor cortex project axons that synapse with motor neurons in the spinal cord.
- The extrapyramidal motor system controls subconscious motor programs and some forms of learning. Neurons in the motor cortex act as feedback circuits, projecting to other areas of the brain, such as the basal ganglia and cerebellum, to send information about intended movement.
- Indirect corticospinal pathways are involved in foundational functions for movement, such as maintenance of background tone in antigravity muscles. Neurons in the motor cortex project axons to areas such as the brainstem, which then project to the spinal cord.

In order for the dog to move his right leg, the left cortex sends signals through the various subsystems to coordinate the movement. Signals of the intended movement travel through the pons to the cerebellum, which combines that information with sensory input, such as proprioceptive input, to coordinate the movement (Norden, 2007, Part 2, pp. 76–77). Signals are sent down the spinal cord to the motor neurons that project their axons to the muscles of the right leg. Excitatory signals cause a specific set of muscles to contract, and inhibitory signals cause the opposing muscles to relax. As a result, the limb moves (LeDoux, 2002, p. 41; Norden, 2007, Part 1, pp. 54–55).

Learning a motor skill involves multiple senses and multiple areas of the brain (Ratey, 2001, p. 204). For a dog to learn to trot in heel position requires the use of his ears to listen to verbal cues, eyes to see the terrain, somatosensory organs to know where his body and limbs are, and muscles in the legs to perform actions in a synchronized manner. What appears to be a simple behavior to teach involves orchestration of the auditory, visual, somatosensory and motor systems.
Two primary areas of the brain that support motor movement are the cerebellum and the motor cortex (Ratey, 2001, p. 163).

The cerebellum is a critical component of the motor system. Its importance is highlighted in that, although it is a fairly small portion of the brain, it contains about half the brain’s neurons (Norden, 2007, Part 2, p. 76). The cerebellum collects information about the body’s movement and position in space, to support equilibrium and posture, regulation and timing of motor movement, and learned skilled motor movement (Norden, 2007, Part 2, p. 76; Ratey, 2001, p. 163). The learning of fine motor skills involves special cerebellar neurons, called Purkinje neurons, which synchronize movement (Norden, 2007, Part 2, p. 77).

When a motor activity is performed often, it recruits a greater area of the brain for its processing (LeDoux, 2002, p. 304). In this way, what a dog does changes the topography of his brain. The neurons in the motor cortex reconfigure themselves with each new motor skill (Ratey, 2001, p. 165). For example, in a study of monkeys taught to maintain hand contact with a rotating disk, the brain regions responsible for touch at the fingertips reorganized; additional neurons were recruited to better support the behavior (Jenkins & Merzenich, as cited in Ratey, 2001, p. 170).

“Motoring through” is a process by which the animal practices the basic motor skills needed to perform the task. The animal learns the behavior through patterning (repetition of a behavior or chain of behaviors), which strengthens neural connections needed to perform that task (Ratey, 2001, pp. 298–299).

Within 6 hours of practicing a new motor skill, the learning can be consolidated and moved from the prefrontal cortex to areas of the brain responsible for permanent motor skills, such as the premotor cortex, posterior parietal cortex and cerebellum. It may be that teaching a second motor skill within this 6-hour window, while the brain is attempting to consolidate the learning of the first motor skill, may impair the learning of the first motor skill (Ratey, 2001, p. 179). More research is needed to support this theory. However, the optimal training plan may be one that teaches a single new motor skill, and then practices already learned motor skills, rather than teaching more than one new motor skill in a single day.

**Physical Exercise**

The most obvious benefit of motor movement is performing goal-directed behavior, to obtain what is needed and avoid what is aversive or dangerous. But movement is beneficial in other ways.

Physiological changes in the brain are required to support learning. Exercise supports these physiological changes by improving blood circulation and lung function, thereby increasing oxygenation, release of glucose, and removal of waste products (Ratey, 2001, p. 35, p. 359).

Learning complex movements strengthens neural circuits in the cerebellum, which can improve balance, coordination and social skills (Ratey, 2001, p. 360). Feedback from motor activity produces neurological development that prepares the brain for further learning (Ratey, 2001, p. 179).

Prolonged rhythmic motor activity, such as 20 minutes of trotting, helps bring the sympathetic and parasympathetic systems into balance. Exercise increases levels of norepinephrine, dopamine and serotonin. This promotes a sense of wellbeing by decreasing pain and providing a feeling of elation, and results in an increase in social responsiveness, motivation, attention and reward-seeking behaviors (Ratey, 2001, p. 314, pp. 360–361). Regular exercise (5 days per week, 1 hour per day) over a period of time (6 weeks or longer) can produce more stable physiological results (O’Heare, 2007, p. 334).

**The Limbic System**

The limbic system is involved in learning, memory, emotion and executive function (Norden, 2007, Part 1, p. 50). Mood and temperament are subject to limbic system activity (Norden, 2007, Part 2, p. 137). It is the limbic system that gives the dog his unique
personality and allows him to engage with the world around him.

The dog’s ability to make decisions, such as in goal-directed behavior, is dependent on functions of the limbic system (Norden, 2007, Part 2, pp. 126–127). Therefore, the limbic system plays an important role in learning.

This system allows the dog to associate emotion, such as pleasure or fear, with various stimuli (Norden, 2007, Part 2, p. 129). If a training session is pleasant, the pleasant emotions are associated with the learning. Place preference, for example, is created when an animal experiences positive reinforcement often in a certain place, and therefore seeks out that place (LeDoux, 2002, p. 245). A positive CER can be created by associating an object (place, person, etc.) with something that elicits anticipation or joy, causing the presentation of that object to elicit the same pleasant emotion.

A negative CER can be created by associating an object (place, person, etc.) with something that elicits pain or fear (Roberts, 1998, p. 128). If a training session is unpleasant or evokes fear, unpleasant or fearful emotions are associated with the learning. If the training session involves both pleasant and unpleasant emotions, both of these are associated with the learning (Rosales-Ruiz, 2007, January).

The limbic system is a complex “super system” that integrates many areas of the brain (Norden, 2007, Part 2, p. 126). It is organized as complex feedback circuits that provide moment-to-moment mood regulation. A few primary components of the limbic system are the amygdala, ventral tegmental area (VTA), hippocampus, hypothalamus, thalamus, nucleus accumbens, orbitofrontal cortex and reticular formation (Norden, 2007, Part 2, pp. 123–136; Ratey, 2001, p. 227). The limbic system is situated alongside the cerebellum and basal ganglia, which are responsible for control of basic movement, primitive reactions, and learned reactions that have become automatic (Ratey, 2001, p. 162).

Various neurotransmitters are involved in the limbic system, including glutamate, GABA, serotonin, dopamine and norepinephrine (Norden, 2007, Part 2, p. 137). Neuromodulators that support the limbic system include opioids and oxytocin (Norden, 2007, Part 2, p. 137).

The limbic system can be activated more quickly than the frontal cortex (Ratey, 2001, p. 314). When the limbic system is active, the frontal cortex is suppressed. Areas of the brain that process learned behaviors—higher brain areas—are suppressed and the areas of the brain that process automatic behaviors—lower brain areas—are activated (Ratey, 2001, p. 172). The dog becomes less able to learn, and less able to process and perform already learned behaviors that have not yet become automatic, and more likely to perform a freeze, flight and/or fight response. This is because the release of norepinephrine and dopamine in the frontal cortex inhibits its activity (Lindsay, 2000, p. 112, cited in O’Heare, 2007, p. 104). Therefore, a dog in a highly emotional state, such as fear, aggression, anxiety or overexcitement, does not learn well.

Alternatively, when the frontal cortex is active, the limbic system is suppressed (O’Heare, 2007, p. 104). If a dog practices known behaviors, the learning areas of the brain become active and the primitive survival-response areas of the brain are inhibited (Norden, 2007, Part 3, p. 59). This is why keeping a dog working on operant behaviors helps reduce emotional reactivity, as long as the dog is not already in an emotionally aroused state.

**Sympathetic and Parasympathetic Nervous Systems**

A dog’s *threshold* is the point at which the dog becomes emotionally aroused. Neurologically, emotional arousal causes the release of various neurotransmitters and hormones that prepare the dog for action. Physiologically, emotional arousal causes responses such as tensing of muscles as the dog becomes ready for action, increase in heart rate and breathing, and pupil dilation. Thresholds vary depending on the breed, individual,
learning history, and current internal state (levels and combinations of various hormones and neurotransmitters).

Emotional arousal is mediated by the sympathetic and parasympathetic nervous systems. These two systems work together to maintain homeostasis in the body, providing the dog with the ability to perform behaviors for survival in a changing environment. Nerves belonging to each of these systems regulate internal organs, preparing them for imminent behavior patterns in response to certain stimuli—for example, responding appropriately in social situations, fleeing from danger, or digesting food (Ratey, 2001, pp. 171–172, p. 229).

The sympathetic nervous system prepares the body for emergency action, such as freeze, flight or fight. In a stressful situation, the sympathetic nervous system is activated. This, in turn, activates a system called the hypothalamic–pituitary–adrenal (HPA) axis, which controls the release of stress hormones. The hypothalamus releases a peptide called corticotrophin-releasing factor (CRF). This causes the pituitary gland to release adrenocorticotropic hormone (ACTH), which causes the adrenal glands (anterior to the dog’s kidneys) to release epinephrine (adrenaline) and cortisol into the bloodstream. Epinephrine results in increased alertness, muscle stimulation, increased heart rate, and other physiological changes that provide a means of defense.

Cortisol acts on various parts of the body to cope with stress (Ratey, 2001, pp. 171–172, p. 229). When it reaches the brain, cortisol binds to receptors in the hippocampus. In a normal individual, the hippocampus will respond by sending signals to the hypothalamus to stop releasing CRF, which halts the release of cortisol. The hypothalamus activates the parasympathetic nervous system, which prepares the body for ongoing regenerative activities such as digestion and immune response. Chemicals that calm the body, such as dopamine, are released. The heartbeat slows, digestion resumes, and the body is returned to its normal state (Norden, 2007, Part 3, pp. 148–149; Ratey, 2001, pp. 171–172, p. 229).

The sympathetic and parasympathetic systems generally maintain homeostasis. However, some animals can be more nervous (have a more active sympathetic system) and some more calm (have a more active parasympathetic system) (Lindsay, 2000, pp. 79–89). A more active sympathetic system results in a lower stress threshold.

**Emotion**

Emotion is a core function of the limbic system. Through emotion, the limbic system guides reasoning and supports social intelligence (Ratey, 2001, p. 292, p. 310).

Emotional information influences attention and working memory processes, thereby biasing decision making (LeDoux, 2002, p. 253). In this way, emotion plays an important role in learning and in executive function (Norden, 2007, Part 1, p. 56).

Emotional arousal causes attention to be focused on the event, and activates areas of the brain involved in processing of that type of event. Emotionally charged information travels from the thalamus to the amygdala through a direct pathway, bypassing the cortex. This inhibits other areas of the brain; resources are redirected to the emotionally arousing event. In this way, any learning that occurs is relevant to the current emotional situation (LeDoux, 2002, pp. 320–322).

Emotion systems learn by association based on respondent conditioning: one stimulus acquires the emotionally-arousing qualities of the other stimulus. The amygdala, temporal lobes, posterior medial orbital cortex and frontal lobes work together to attach emotional significance to stimuli (Ratey, 2001, p. 313).

Response to emotion systems can become operant when the animal chooses to take action to either avoid or approach the stimulus (LeDoux, 2002, p. 303). Components interconnected with the limbic system, such as the anterior cingulate gyrus, are involved in
motivation and choice behavior (Ratey, 2001, p. 165).

Memories of emotional events are processed independently of the events with which they are associated (Ratey, 2001, p. 211). This makes the encoding and retrieval of emotionally charged memories different from that of non-emotional memories (Ratey, 2001, p. 209).

There is a close relationship between emotion and movement (Ratey, 2001, p. 162). Both these words have their roots in the Latin word *movere*, meaning “to move” (Ratey, 2001, p. 227, p. 247). Movement resulting from emotional input is under different control from movement resulting from activity of the cortex (Ratey, 2001, p. 175). Outward movements that result from emotion include everything from facial expression to erection of body hair to fleeing from predators (Ratey, 2001, p. 228).

**Pleasure**

The *endogenous reward system* is responsible for the subjective experience of pleasure. This system detects novelty and assigns emotional value to rewarding stimuli. Operant responses are motivated by reinforcers because of the endogenous reward system (LeDoux, 2002, p. 246).

Learning and motivation are intertwined (LeDoux, 2002, p. 237). Motivation is goal directed, and learning is the means of knowing how to achieve a specific goal (Ratey, 2001, p. 247).

Goal-directed behavior involves many areas of the brain, for processing perception of both internal and external stimuli, assessment using current and stored information, and the motor ability to respond. Goal-directed behavior involves decisions based on emotion (Ratey, 2001, p. 244). A behavior that leads to positive reinforcement, for example, evokes pleasure in the endogenous reward system, so that behavior becomes operant (Norden, 2007, Part 2, p. 173).

The endogenous reward system is activated during events that bring pleasure and contribute to a sense of wellbeing, such as when seeking food or a mate, or during aerobic exercise. Anticipation paired with uncertainty results in the greatest activation of the endogenous reward system (Norden, 2007, Part 2, p. 174). This is why intermittent schedules of reinforcement are effective in maintaining a learned behavior.

Feelings of anticipation and pleasure are caused by monoamines in the areas of the brain that make up the endogenous reward system (Norden, 2007, Part 2, p. 164). The system is governed by a group of neurons that contain dopamine. This includes the VTA, nucleus accumbens, and orbitofrontal cortex (Norden, 2007, Part 2, pp. 164–166). The nucleus accumbens is connected to the amygdala and is involved in the control of movement—a link between emotion and motivation (LeDoux, 2002, p. 247).

Acquisition of something rewarding, including the reinforcement of avoiding an aversive, is associated with dopamine activity. Dopamine invigorates behavior by activating motor systems, and directs behavior by activating the amygdala and other motivational systems, such as the endogenous reward system (LeDoux, 2002, p. 249; Norden, 2007, Part 2, p. 171). Because of its role in the endogenous reward system, dopamine is important for the associative functions of learning.

The hypothalamus, septum and nucleus accumbens are several such pleasure centers, and each of them use dopamine as a neurotransmitter (Ratey, 2001, p. 243). The VTA consists of dopamine-containing neurons in the midbrain that are involved in the endogenous reward system (Norden, Part 2, p. 123).

Dopamine is more involved in anticipatory behaviors, such as seeking food or mates, than in actual consumption (LeDoux, 2002, p. 246). A reinforcer can, therefore, be made more valuable when it is accompanied by anticipation—for example, marking the behavior with a clicker, then immediately beginning the act of delivering the food slowly. Alternatively, the food can be rolled on the floor to encourage a chase, as long as this does not distract the dog from the
learning. These techniques make the act of delivering the food, in and of itself, highly reinforcing for the dog (Laurence, 2007).

Other pleasure neurotransmitters involved in the endogenous reward system are serotonin (a monoamine) and endorphins (Ratey, 2001, pp. 116–117).

The nucleus accumbens is connected to the limbic system, midbrain and forebrain. The outer shell of the nucleus accumbens, part of the extended amygdala, appears to be important in attention, motivation and learning (Ratey, 2001, p. 244).

The nature of the expected reinforcer defines the nature of the dog’s “central emotional state” (Domjan, 2003, pp. 193–194). Punishment elicits a central emotional state of fear, whereas positive reinforcement elicits a central emotional state of hope. Fear and hope drive very different species-specific behavior systems; therefore, the consequence is an important consideration in operant conditioning.

Motivation is a means to achieve desirable goals and avoid undesired situations (LeDoux, 2002, p. 238). This is the basis of operant learning.

The senses perceive internal and external stimuli. The cingulate gyrus assesses the stimuli, with the help of the limbic system, and compares the results to stored memory. Conflicting goals are assessed, and the dog chooses to inhibit or exhibit behavior in order to seek positive reinforcement or avoid punishment (Ratey, 2001, p. 248).

**Fear**

Fear has an important biological role in keeping the dog safe from injury or death. Fear response has special attributes to support this biologically important role (LeDoux, 2002, p. 124; Lindsay, 2000, pp. 219–220):

- Some fears are biologically prepared and can be learned in one pairing, particularly as a result of an event that is—from the dog’s subjective perspective—traumatic.
- Fear is easily generalized to other, similar, stimuli.
- Fear learning endures, possibly for a lifetime.
- Fear responses are elicited, not emitted. They occur reflexively (LeDoux, 2002, p. 236).

Sensory cells, such as auditory, olfactory and vision receptors, are closely connected to the amygdala. Innate associations of specific responses to specific stimuli are held in the brainstem, which is also connected to the amygdala, providing reflexive response. Direct connections flow from the amygdala to rapid response systems, which provide immediate control of the body. These systems initiate physiological changes such as increased heart rate and release of stress hormones, resulting in activation of the defense system (LeDoux, 2002, p. 161, pp. 288–289; Norden, 2007, Part 3, p. 53).

The amygdala ignores most input, through inhibition of cell firing produced by GABA. What is ignored and what is not depends on both innate and learned associations. When a stimulus is detected that signifies a biologically significant event (such as danger), enough glutamate is released to overcome the inhibitory effects of GABA, and the projection cells begin to fire. This initiates firing of cells in other parts of the brain, resulting in response. This excitation also results in firing of GABA cells, leading to an increase in GABA, which eventually calms the system down. Serotonin facilitates inhibition by exciting GABA cells, resulting in an increase in GABA (LeDoux, 2002, pp. 61–63, pp. 86–87). Different dogs can have different thresholds of arousal, in part because GABA production differs.

In an emotionally charged situation, a specific stimulus often stands out (LeDoux, 2002, p. 215). It is not always the stimulus that caused, or has any connection with, the emotional situation. With associative conditioning, intentional or otherwise, a stimulus can acquire the ability to elicit strong excitation of the amygdala, overriding the GABA produced in the lateral nucleus. This opens a floodgate of
emotional reactivity (LeDoux, 2002, p. 215). Because of the power of associative conditioning, physical punishment, or any other consequence that causes pain or fear, should be avoided.

Because of the biological importance of the defense system, if a dog is above fear threshold, it is ineffective and inhumane to expect him to perform an operant behavior contrary to his defense mechanisms. For example, asking the dog to sit, heel or lie down and ignore the threat will only serve to reduce his trust in the handler and his environment and increase negative associations. It is more effective to remove the dog from the stressful situation and allow his body to return to homeostasis before requesting operant behaviors, then manage the environment so that he is unlikely to experience fear (L. Clifton-Bumpass, personal communication, October 18, 2007).

**The Effect of Stress on Learning**

Mild stimulation of the sympathetic nervous system triggers the release of noradrenaline, which facilitates memory consolidation (Joels, Pu, Wiegert, Oitzl, & Krugers, 2006, p. 154). Because of this, a small amount of stress having continuity and context with the association to be learned can focus attention, facilitating learning (Joels et al., 2006, p. 152).

Although minor stressors can facilitate learning, traumatic or chronic stress causes physiological changes that impede learning (Joels et al., 2006, p. 154). Traumatic or chronic stress results in high levels of cortisol. Cortisol before or during an event can suppress LTP (Joels et al., 2006, p. 164).

A super-LTP moment, when a multitude of detail is stored in memory (called “flashbulb memory”), can be created during a traumatic event. However, the cost to the dog’s ability to learn overall is high (Ratey, 2001, p. 192). Traumatic events can lead to chronic stress, which damages the nervous system.

Dogs that are exposed to traumatic or repeated stressful events, such as use of any stimulus that elicits pain, fear or anxiety, can maintain chronic levels of stress. Under chronic stress, the body’s ability to maintain homeostasis begins to fail (Norden, 2007, Part 3, p. 149). Dogs under chronic stress are incapable of higher-level learning.

During chronic stress, cortisol remains elevated in the bloodstream. This causes increased neural activity. Neurons in the hippocampus bind with cortisol, leading to overexcitation. These neurons are depleted of glucose, which leaves them susceptible to damage caused by glutamate during the increased neural activity. Dendrites shrink and the neurons begin to die. In addition, neurogenesis (production of new neurons) ceases. As a result, the hippocampus shrinks. Working memory and spatial memory, which rely on the hippocampus, are adversely affected (LeDoux, 2002, pp. 278–279; Norden, 2007, Part 3, p. 149; Ratey, 2001, p. 211, p. 218).

Elevated levels of cortisol cause other damage as well. Neurotrophic factors, required for cell growth and synapse maintenance, decrease (LeDoux, 2002, p. 280). The body’s immune system becomes depressed, DNA repair mechanisms decrease, and autoimmune mechanisms increase (Norden, 2007, Part 3, p. 149). Cortisol modulates serotonin’s ability to excite GABA cells; therefore, elevated cortisol results in increased fear response (LeDoux, 2002, p. 64).

Traumatic or chronic stress also causes other chemical imbalances, such as depleted levels of serotonin, a chemical responsible for mood regulation. In both dogs and humans, this can result in disrupted sleep cycles, decreased immunity, inability to think rationally, oversensitivity to pain, lethargy and inability to experience reward or pleasure (O’Heare, 2003, pp. 13–26).

As a result of traumatic or chronic stress, learning and higher thought processes are temporarily suspended (O’Heare, 2003, p. 19). The prefrontal cortex becomes less active, as control of the neurological system is taken over by the defense system (Norden, 2007, Part 3, p. 59).
Impulse Control

Impulse control is choice behavior. Impulse control is learned when the dog begins to understand that self control is reinforced, and that delaying gratification is highly reinforcing (O’Heare, 2007, pp. 330–331).

Impulse control, and the ability to understand the consequences of behavior, involve the orbitofrontal cortex (Norden, 2007, Part 2, p. 132). Because activation of the limbic system suppresses processing in the frontal cortex, impulse control is difficult when the dog is in a highly emotional state. In order to practice impulse control, and avoid practicing impulsive behaviors, the dog should be kept below emotional thresholds. Emotional thresholds include excitement as well as fear.

Impulse control is an innate skill that is used, for example, in stalking behavior. As with any other skill, the neurons and muscles used for impulse control develop through practice. Dogs learn impulse control, not by practicing quiet behavior, but by practicing impulse control and then being allowed to achieve either the reinforcer they seek, or a reinforcer of higher value (Laurence, 2007).

Dogs can be taught to practice impulse control by tapping into stalking behavior through play exercises. For example, in the “whippits” play exercise, a toy is tied to the end of a rope attached to a lunge whip. The dog is allowed to chase the toy, but is only allowed to catch the toy if he stops to stalk it. When the dog stops to stalk, the toy lies still. If the dog is still for a moment or two, the toy jumps within the dog’s reach (Laurence, 2007).

Teaching the dog basic skills such as focus, puzzle solving and body awareness will help him develop cognitive abilities that can be utilized instead of emotional responses, helping him learn to mediate his own level of arousal in any given situation (Laurence, 2007).

Dogs can display self control in many social situations. For example, when encountering an unfamiliar dog, person or situation, a dog may stop to consider a situation before moving forward. These “ponder” moments can be marked and reinforced using clicker training, causing them to become part of the dog’s repertoire, therefore making self-control behaviors more probable.

Ponder moments can be used as a starting point to teach puppies an awareness of, and appropriate responses to, human body language (Laurence, 2003). By marking and reinforcing the correct response to a specific type of body language, the trainer can teach the puppy to recognize when a person is approachable and when a person should be ignored. For example:

- A person walks toward the puppy with arms folded or shoulders squared, perhaps striding quickly, not making eye contact. The puppy is clicked when he shows any “ignore” behavior, such as backing up a step, sitting quietly, or looking away.
- A person walks toward the puppy with arms outstretched or relaxed, and faces the puppy, perhaps making cooing “cute doggy!” sounds. The puppy is clicked and reinforced for interactive behavior such as moving forward a step, sitting, or making eye contact with the person.

Clicker-avid dogs sometimes find that throwing behavior is more reinforcing than stillness. To avoid continuous offering of behaviors, and to encourage impulse control, still behavior should be reinforced as often as necessary to make it a reinforcing choice (Laurence, 2005).

The Neurology of Critical Development Periods

How the brain develops is epigenetic: a result of both genetic and environmental influence (LeDoux, 2002, p. 82). It is thought that genes account for less than half of any given behavioral trait (LeDoux, 2002, p. 91). Because of the brain’s plasticity, particularly in the formative period but also throughout life, environment plays an important role (LeDoux, 2002, pp. 66–67). Genes are switched on or off in response to environmental conditions. Genes
make proteins, and these proteins affect the activities of other genes (LeDoux, 2002, p. 93).

Genes predispose, but they do not predetermine, how the brain becomes wired (LeDoux, 2002, p. 296). For example, dogs may be predisposed to predatory behaviors such as chase, grab and bite. But if livestock-guarding dogs that show predatory behavior are removed from livestock (and so are not allowed to practice the behavior) during the window of neurological development for this behavior in their breed (about 6 months of age), the behavior will fail to develop and they can later be returned to the herd (Coppinger & Coppinger, 2001, p. 221). Practicing the stimulus–response of eye-stalk behavior during the time the neurons that support this behavior are forming builds a stronger eye-stalk behavior. Without this practice during that window of time, eye-stalk behavior may not form.

A critical development period is a window of time during which specific stimuli produce long-term effects on behavior and effects that are resistant to change (Serpell & Jagoe, 1995, p. 82). If exposure to certain types of stimuli does not occur during a critical development period, specific learning opportunities are lost (Beaver, 1999, p. 137). Once the window closes, normal development cannot occur for that particular perceptual system or skill. Missed development in one area can affect other areas, causing them to develop abnormally (Norden, 2007, Part 1, p. 101).

The inherent plasticity of the neurological system allows changes in brain structure to continue on a moderate scale throughout a dog’s life. However, early development is a time of substantial growth in the brain’s structure. This growth includes the organization of neurons (the brain’s gray matter) and the formation of myelin (the brain’s white matter). This initial development provides a lifelong foundation for learning. It is why early exposure to as many varied stimuli as possible, including new people, environments, sights, sounds and smells, is critical to a pup’s successful integration into society (Fields, 2008, pp. 56–57; LeDoux, 2002, p. 96; Lindsay, 2000, p. 35).

In the early stages of life, the brain is organizing itself, forming connections in response to both internal and external stimuli (Ratey, 2001, p. 23). As the brain takes shape, neurons multiply, segregate, and then differentiate into about 150 types. The tips of growing axons form growth cones (Nicholls et al., 2001, p. 497). As each axon elongates, it navigates toward its final destination, guided by chemical trails formed by glial cells that act as attractants or repellants (Nicholls et al., 2001, pp. 501–502). As they travel to various sites in the body, axons connect with other neurons or sensory cells along the way. For example, the axon of a visual neuron may grow from the visual cortex, located at the back of the brain, to meet a visual receptor, located behind the eyes. The axon of a muscle neuron may grow from the spinal cord to innervate a leg muscle (Nicholls et al., 2001, p. 501), and so on. Chemicals in the environment, both internal and external, can affect the growth of these neurons (LeDoux, 2002, pp. 68–69).

There are critical periods of neural development when growth and survival of neurons require proteins known as growth factors. Once the neurons are mature, growth factors are needed to regulate vital chemicals such as norepinephrine (Nicholls et al., 2001, p. 512).

After the axons have formed, they are myelinated (surrounded by a fatty protective coating called a myelin sheath) by glial cells (Norden, 2007, Part 1, p. 35). Myelination, which protects the neuron and increases the speed of the signal moving down the axon, occurs during the formation of the nervous system, and is not complete until long after birth (Norden, 2007, Part 1, p. 97, p. 125). The amount of myelination, and the nodes between myelin along the axon, dictate the speed of signal transmission. In this way, information reaches consolidation areas of the brain at precisely the correct time to form correct associations (Fields, 2008, p. 59).

Myelination in different areas of the brain occurs at different ages. Generally, myelination proceeds from the back of the brain to the front.
Myelination of the frontal lobe does not take place until just prior to adulthood (Fields, 2008, p. 56). This is one reason juveniles lack impulse control.

More practice of a particular skill, especially at a young age while the brain is largely forming, produces more myelination in the areas of the brain that support that skill. Those areas become “packed” with myelin. Once an axon has been myelinated, the changes that can occur are limited (Fields, 2008, p. 57).

The mammalian brain has billions of neurons. Before birth, an animal has more neurons than it needs. In early life, regressive events occur: neurons that are weak, or that don’t have proper connections with other neurons, are pruned. As a result, only about half of the original neurons survive. Regressive events occur as a result of both environment and genetics, to fine tune the neurological system for the functionality it needs in the current environment (Norden, 2007, Part 1, p. 135). Pruning of unused neurons and strengthening of stimulated neurons continues, on a smaller scale, throughout life (LeDoux, 2002, p. 74; Norden, 2007, Part 1, p. 107; Ratey, 2001, p. 26).

The internal and external environment affect whether or not certain neurons will live and others will die, which connections the surviving neurons will take, and so on. Stimulation, through experience, provides the nutrients neurons need to survive (Ratey, 2001, pp. 23–26). When an action potential occurs, the postsynaptic cell releases molecules called neurotrophins, which promote survival and growth of a neuron. Neurotrophins are taken up by the presynaptic cell, strengthening it (LeDoux, 2002, pp. 80–81). With stimulation, axons and dendrites branch and sprout new synaptic connections. Without stimulation, a neuron does not receive neurotrophins. Without neurotrophins, the neuron will retract and die. This is referred to as “neural Darwinism” (Edelman, 1987, cited in LeDoux, 2002, p. 73). Neural evolution is economical: it ensures that only the neurons necessary for the neurological system to function in the animal’s environment survive, and that these neurons have the space and nutrition needed to continue to survive (Ratey, 2001, p. 280).

Perception is an important part of experience. Experience, through stimulation of all of the animal’s senses, is particularly important during the critical periods of development. Each sense has its own time window for development, during which the neurons that connect to the sensory organs are organizing themselves. Use of the sense during the development window strengthens the neurons that support that sense, defining the ability to use that sense for the remainder of the animal’s life. Senses that are enriched with a variety of stimulation during development will form stronger connections, with more synapses (Ratey, 2001, p. 35, p. 40).

If there is a disturbance in one of the senses during the period when that sense is being formed, it could impair development of that sense (Ratey, 2001, p. 54). For example, if one eye is covered with an eye patch during the development of sight, the neurons destined for the covered eye will retract and die. The neurons destined for the uncovered eye, which is receiving stimulation, will take over the territory left vacant by the neurons that retracted. If the covered eye does not receive stimulation during development of neural connections for sight, it will never gain the ability to see (Hubel & Wiesel, 1962, cited in LeDoux, 2002, pp. 76–77).

The adult brain has a subtle plasticity, supporting learning as a result of experiences throughout life (LeDoux, 2002, p. 96). The immature brain has extensive plasticity. Because the brain continues to grow and organize itself until just past puberty, behaviors are more easily learned at a young age. What the dog is exposed to during the formation of the neurological system affects that formation (Ratey, 2001, p. 340). Animals raised in enriched environments have significantly more synapses than those raised in a bare environment (Norden, 2007, Part 3, p. 31). This is why experience, through exposure to various stimuli during the critical periods of a puppy’s life, is so important. These experiences help determine which
neurons survive and thrive, and which axons are more heavily myelinated.

**Critical Development Periods of the Domestic Dog**

The critical periods of development identified for dogs can be identified as prenatal, neonatal, transition, socialization and juvenile. The age during which each period occurs varies between breeds and individuals, and some of these stages overlap (Serpell & Jagoe, 1995, p. 83). There are also adult and geriatric phases. However, these are not generally considered as critical as the other five periods, because the basic formation of the neurological system occurs from the prenatal period through puberty.

**Prenatal Period**

The prenatal period occurs while the pup is in the womb. Neurons are generated, and their basic patterns develop before birth (Norden, 2007, Part 3, p. 17).

Transplacental maternal influences affect the formation of the fetal nervous system (Serpell & Jagoe, 1995, p. 80). For example:

- Pups may be more reactive if the bitch is subjected to stressful experiences during pregnancy. This is thought to be caused by the effects of stress-related hormones, such as corticosterone, on the developing fetus (Serpell & Jagoe, 1995, p. 80).
- Androgens in the womb, either from the mother or from male siblings, have been found to promote masculine traits in the offspring of female rats and mice. There may be a similar effect in dog pups (Serpell & Jagoe, 1995, p. 80).
- The gustatory receptors (taste buds) are developed before birth. Chemicals present in the amniotic fluid can affect these receptors, affecting the pup’s food preferences (Thorne, 1995, p. 108).

Because of potentially lifelong effects on a pup’s health and behavior, pregnant bitches should be kept in a low-stress environment and fed a variety of nutritious foods.

**Neonatal Period**

The neonatal period occurs from birth to approximately 2 weeks of age. During the neonatal period, the eyes, ears and motor skills are not yet fully developed, so the puppy uses his sense of touch, smell and taste to experience the world (Serpell & Jagoe, 1995, p. 80).

For innate behaviors to develop properly, they must be practiced within the critical development windows. For example, a puppy prevented from nursing within the first hours of birth may not develop the ability to nurse (Coppinger & Coppinger, 2001, p. 220).

For perception to develop normally, pups need to experience a variety of stimuli during the neonatal period. Puppies handled daily and exposed to noxious physical stimuli, such as cold, for short periods were found to develop coats faster, grow faster, develop motor skills and problem-solving ability earlier and open their eyes earlier. When tested in strange situations at a later age, pups exposed to various stimuli in the first 5 weeks of life were more confident, had better resistance to stress, were more emotionally stable and learned more easily. This suggests that early exposure to minor stressors produces adaptations in the dog’s pituitary–adrenocortical system that allow him to cope more effectively in stressful situations (Serpell & Jagoe, 1995, p. 81).

During the neonatal period, breeders should have a program of puppy handling to encourage the pups to develop stability and resilience. Once a day for 3 minutes, each pup should be briefly exposed to mild stressors such as cold temperature and gentle back-and-forth rocking (Lindsay, 2000, p. 37).

**Transition Period**

The transition period occurs at the age of about 10 to 16 days and lasts for about a week. This period consists of a rapid transformation during which the patterns of neonatal behavior are replaced by more mature traits (Serpell & Jagoe, 1995, p. 81).

During the transition period, the eyes and ears open and the pup begins to gain motor skills...
such as the ability to crawl forward and backward, stand, walk and play-fight with littermates. He begins to show tail wagging and other social signals. He also begins to defecate and urinate without stimulation (anogenital licking) from his mother (Serpell & Jagoe, 1995, p. 81). The pup may also begin to stray from the nest box and eat solid food (Beaver, 1999, p. 138).

As with humans, some memories formed when the pup is very young may be subject to infantile amnesia (Roberts, 1998, p. 199).

Socialization Period

The socialization period occurs roughly between 3 and 12 weeks of age (Beaver, 1999, p. 138). There is a peak sensitivity between 6 and 8 weeks of age (Serpell & Jagoe, 1995, p. 83).

The socialization period is marked by maturation of physical, neurological, and behavioral features (Beaver, 1999, p. 138). The pup’s brain begins to develop in the womb, and continues developing after birth. There are morphological changes during the puppy’s first 6 weeks of life, such as increasing brain size. There are also physiological changes, such as the appearance or disappearance of various reflexes (Beaver, 1999, p. 69).

Between 2 and 5 weeks of age, the pup’s hearing and sight develop. The eyes and ears open at about 2 weeks of age, and myelination of the visual and auditory cortex begins (Beaver, 1999, pp. 44–45, p. 72).

From 3 to 5 weeks of age, pups actively approach novel objects, including other dogs or people. Above 5 weeks of age, they become more wary of novel objects. This wariness peaks at about 12 to 14 weeks of age (Beaver, 1999, p. 138).

Social behaviors, such as attention- and care-soliciting, are learned during the period between about 4 and 14 weeks of age (Serpell & Jagoe, 1995, p. 83). Bite inhibition is also learned during the socialization period. As puppies play with each other, a hard bite from one pup will cause the other pup to yelp and immediately stop playing. The other pup learns that, in order to continue play, he must control bite pressure (Beaver, 1999, p. 59).

During this period, dogs form primary social attachments (Serpell & Jagoe, 1995, p. 81). The socialization experience determines the species with which the dog identifies. For example, livestock-guarding dogs housed with sheep during the socialization period develop a lifelong social bond with sheep (Coppinger & Coppinger, 2001, p. 104). If a puppy is exposed to other dogs and to humans during the socialization period, the pup will identify with both species (Serpell, 1995, p. 246). A dog who is not socialized during this period will be socially handicapped for the remainder of his life (Beaver, 1999, p. 140).

Some hunting and herding dogs develop predatory behaviors, such as eye–stalk–chase, during the socialization period. With these breeds, predatory behaviors such as eye–stalk are incorporated into social play (Coppinger & Coppinger, 2001, p. 116, p. 204).

Pups normally experience various stages of fear during the socialization period. The onset of wary or fearful behavior is thought to be a response to the start of stable learning (Beaver, 1999, p. 139). Pups initially begin to experience wariness and fear between 8 and 10 weeks of age. However, the onset and duration varies between breeds, and between individuals, due to individual development rates (Coppinger & Coppinger, 2001, p. 115). Pups not exposed to various stimuli during the socialization period develop neophobic responses that carry through adult life (Serpell & Jagoe, 1995, p. 96).

During this period, dogs develop lifelong coping mechanisms for novel stimuli. To provide a strong social foundation, breeders and dog guardians should plan controlled exposure to as many different types of stimuli as possible, beginning at about 3 weeks of age. The socialization plan should include exposure to various sounds, scents, environments, people and other dogs.
If possible, guardians should visit the litter of pups from the age of 5 weeks onward, handling the chosen pup to allow bonding to occur (Coppinger & Coppinger, 2001, p. 113). To avoid weight loss and increased risk of disease, and to ensure social skills are developed through interaction with the litter, pups should not be adopted until they are over 6 weeks of age (Beaver, 1999, p. 140).

Between the age of 8 and 12 weeks, puppies should be exposed to circumstances and conditions they are likely to encounter as adults (Serpell & Jagoe, 1995, p. 83). Exposure of as little as a couple of 20-minute sessions per week is sufficient for socialization to occur (Serpell & Jagoe, 1995, p. 82). During fear periods, exposure to novel stimuli should be reduced to a level where the pup is able to quickly recover and investigate. Fear periods should be avoided when planning necessary traumatic events, such as adoption or vaccination (Beaver, 1999, p. 139). In addition to social skills, pups should be given opportunities to continue to develop perception skills. For example, various surfaces to walk on and safe but challenging objects to climb help develop proprioception (Laurence, 2007).

Although there is a risk of exposure to disease during the first few months of life, the lifelong benefits of socialization outweigh the risk. Puppy parties can be organized to facilitate socialization. Parties should include a variety of novel stimuli, such as people with costumes and hats, children, elderly people, wheelchairs, balloons and umbrellas (Dunbar, 2003).

Pups learn lifelong skills during the socialization period, such as attention, self control and dog communication. Basic training during this period should include positive reinforcement of attention and impulse control. Puppies should be socialized in puppy classes with instructors that are knowledgeable in domestic dog behavior and learning theory.

Play builds social bonds, enhances social skills, relieves stress, strengthens physical coordination and hones motor skills (Ratey, 2001, p. 181; Zink, 2006, Part 7). Play between puppies/dogs that are familiar with each other is recommended. However, free play between puppies that are not familiar should be carefully considered. This is because the situation cannot be controlled, so the learning cannot be controlled (Laurence, 2007). Puppies who are bullied, even on a few occasions, can learn to be fearful. Puppies who bully successfully can learn to be more efficient bullies. Unless dog-to-dog play is what that dog’s normal environment provides, puppies need to learn to communicate with each other, but not necessarily to play with unfamiliar dogs. It is far better to socialize puppies in a controlled manner—for example, by reinforcing polite and appropriate forms of greeting.

### Juvenile Period

The juvenile period begins at about 12 weeks of age and lasts until sexual maturity (Beaver, 1999, p. 140).

Near the start of the juvenile period, the primary socialization window comes to a close, and the pup may become less tolerant of change. However, socialization should continue through the juvenile period to keep social behaviors strong (Beaver, 1999, p. 140).

Predatory motor patterns such as eye, stalk, chase and bite begin to display at about 7 months of age in most breeds (Coppinger & Schneider, 1995, p. 27). However, some breeds exhibit predatory behaviors much earlier. For example, border collies can begin to exhibit eye–stalk at around 8 weeks of age (Coppinger & Coppinger, 2001, p. 314).

During the juvenile period, social, physical and psychological skills are practiced and perfected. For example, the male dog may begin to raise his leg to urine mark (O’Heare, 2005, p. 31).

Puberty occurs between 6 and 18 months, slightly later in males than in females (Beaver, 1999, p. 200). At around 6 to 8 months, males experience a surge of testosterone (Lindsay, 2005, p. 306). Sex hormones are critical to the dog’s development, such as growth plate closure of the long bones and modulating emotional
reactivity. Because of this, neutering (spay or castration) before maturity (approximately 14 months of age) is not recommended (O’Heare, 2007, p. 347; Zink, 2006).

Behavior during the juvenile period, particularly as the dog becomes sexually mature, may be overly energetic and erratic, so the dog may have difficulty practicing self control. Hormone levels may play a role, since intact adolescent males produce several times the amount of testosterone as normal adults. Females, also, have hormonal fluctuations as they prepare for their first season (Diamond-Davis, 2004). During puberty, the prefrontal area of the brain is reorganized under the influence of hormones (Norden, 2007, Part 3, p. 17).

As with the socialization period, basic training during the juvenile period should include positive reinforcement of attention and impulse control. During this time, management of the dog and his environment should be used to avoid practice of undesired behaviors (Laurence, 2007).

### The Neurology of Learning Principles

Attention (and therefore learning) can be affected by establishing operations, antecedents, salience of the stimulus and value of the reinforcer.

**Associative Learning**

Associations are vital for survival, because they allow the dog to predict different outcomes of certain responses in certain contexts (Roberts, 1998, p. 122)—for example, associating the scent of prey with hunting behaviors, and associating the scent of estrus with mating behaviors. Because of its evolutionary importance, association is a core function of the neurological system.

The memory of one event includes multiple components of perception, distributed throughout the brain (Ratey, 2001, p. 199). The various components of perception are glued together as one consolidated memory by the process of association, which allows the dog to link together stimuli that occur contiguously in time and space (Roberts, 1998, p. 165). For example, when the trainer praises the dog, she may also look at him with soft eyes, stroke his head gently, and say “good dog.” The dog’s
memory of the trainer praising him may include visual, auditory, olfactory and somatosensory information.

Associations are made between stimuli, as well as between the absence of stimuli (Roberts, 1998, p. 133).Contextual stimuli, such as the surrounding environment, can also be included in the association of an event. This is because the hippocampus, which is aware of unattended background stimuli, is synaptically connected to the brain systems that mediate conscious awareness (LeDoux, 2002, pp. 131–132).

Certain associations are contraprepared, so learning them is more difficult. For example, dogs are biologically prepared to provide a predatory response to sudden, fast movement. However, “sit” is not part of the normal predatory response. Therefore teaching “sit” in response to a jerky, fast hand signal is not as easy as teaching sit in response to a calm, slow hand signal.

Associations are most easily learned when stimuli are contiguous (occur closely in time), are either similar or contrasting, occur frequently and are salient to the subject, such as when reinforcers result (Roberts, 1998, pp. 122–123). Some associations, particularly those that are biologically prepared or are linked with perceived life-threatening situations, can be learned in one experience. This is called one-trial learning (Roberts, 1998, p. 168).

Once an association is made, it can become generalized to other members of the same stimulus or response categories (Roberts, 1998, p. 358). This is the process of generalization. A cue is generalized if the dog is likely to perform the response if the cue is altered (Roberts, 1998, p. 142). For example, the dog sits when a verbal cue is given by various people.

There are various types of association. For example, cognitive mapping refers to the association of stimuli in space, and sequential mapping refers to the sequential association of stimuli (Roberts, 1998, p. 121).

Dogs have the ability to learn the order of events. This is called serial learning. Serial learning is important for motor function, which involve precise sequences of muscle activation (Roberts, 1998, pp. 266–267). In serial learning, the first response becomes a cue for the second response, which becomes a cue for the third response, and so on (Roberts, 1998, p. 268). Serial learning is apparent in any behaviors that involve sequences of movement—for example, dog sports such as obedience, agility, freestyle and flyball. Although dogs can respond to sequential and contextual cues, they may or may not be aware (have a “map”) of the entire sequence (Roberts, 1998, p. 276).

Dogs can also learn associations based on both absolute and relational properties (Roberts, 1998, p. 163). For example, dogs can learn to choose a specific article out of three (absolute association) or to choose the article that is the same as the one presented (relational) (Ramirez, 2007).

Not all learning is immediately apparent. Some behaviors can be learned even though it appears no learning has taken place. This is called latent learning. Spatial learning provides a good example of this (Roberts, 1998, p. 160). While the dog is investigating new surroundings, he may be building a cognitive map. This learning may be apparent only later, when something of value is available to the dog for navigating this environment.

**Hebbian Plasticity**

Donald Hebb’s theory of neural plasticity, referred to as Hebbian plasticity, explains the phenomenon of associative memory in terms of synaptic connectivity. For example, neuron $N$ is postsynaptically connected to two other neurons: $S$, a strongly connected neuron, and $W$, a weakly connected neuron. Neuron $N$ is likely to fire when $S$ fires, but not when $W$ fires. However, if both $S$ and $W$ fire together, $N$ will fire, which will strengthen connections from $N$ to both $S$ and $W$. This strengthens $W$, and leads to a pairing of $S$ and $W$ (LeDoux, 2002, pp. 135–137).
Continuity and context are important because hormones and neurotransmitters need to be released near the relevant neural circuits involved in processing the memory, at the time the neurons are firing, in order to facilitate long-term potentiation (Joels et al., 2006, pp. 154–155).

Responses can be primed through this phenomenon, because the connection between two neurons is strengthened if the postsynaptic neuron is already active when the presynaptic neuron fires (LeDoux, 2002, pp. 135–137). The speed of perception can be increased by this type of priming (Roberts, 1998, p. 42). For example, a novel sound will prime the dog to better hear subsequent sound.

If certain contextual cues are strongly associated with specific behaviors, the dog will be primed to perform those behaviors in that context. For example, the sight of a tunnel or the sound of a teeter banging can prime a seasoned agility dog for an agility run. Unfortunately, contextual priming often backfires if the dog becomes so overwhelmed with excitement that he cannot follow basic handler cues.

Due to the neurology of association, the discriminative stimulus, response and reinforcer are connected in the dog’s mind. Careful and thoughtful planning of the cue, behavior and reinforcement (including placement of the reinforcement) will help build correct behavior (Laurence, 2007). For example, if a behavior such as left-side heelwork is reinforced by feeding from the right hand, the dog may position his head in front of the handler to receive the food from the right hand after the click. The head coming around to the front of the handler will become part of the heelwork behavior. If this is an unwanted behavior, then it should be avoided in training.

Choice of a cue for a behavior should be made with the dog’s perceptions in mind. Something that is salient to the handler may not be salient to the dog. For example, in teaching the dog to select a specific object from a group of objects, color may be salient to the handler. However, contrast or scent may be much more salient to the dog.

A set of small, consistent cues, taught to proficiency, is the most effective means of initiating behavior. Be complementary, not contradictory, in your body postures when working with the dog. Cues as subtle as the balance of the body can be used, if trained. For example, in heelwork, the careful and consistent turning of the shoulders (before changing direction) should be enough to cue the dog that the handler is about to turn (Laurence, 2007).

**Poisoning the Cue**

Respondent conditioning, a powerful means of associative learning, can cause pairing of punishment with environmental stimuli at the time the punishment is delivered. This can lead to directed or generalized fear. For example, if
the dog forges out of heel position to greet another dog, and the trainer responds by jerking the leash and commanding “heel”, the dog may associate any or all of the stimuli in the environment with fear and pain. Associated stimuli may include the sight and smell of the other dog, the sight and smell of the trainer, the sound of the cue “heel!”, and the sights, sounds and smells of the general environment. This is how cues, including contextual cues, can become poisoned. Resulting negative associations can lead to fearful or aggressive responses to one or more of the stimuli at a later time. For example, the dog may learn to respond aggressively upon sight of other dogs. Poisoning of cues is not yet well understood. However, because of the associative properties of learning, it is wise to avoid punishment in training (Pryor, 2002).

**Memory Retrieval**

It is possible for a memory to be available, but not be accessible. If the cue was not strongly associated with the behavior, the cue may not prompt the behavior. Cues can be multidimensional, involving both external and internal stimuli. For example, ambient stimuli such as lighting, scent and background noise may be part of the contextual picture associated with a specific behavior. The reinforcer can also become part of the contextual picture.

A dog’s internal state fluctuates throughout the day, in response to both the internal and external environments (Roberts, 1998, p. 193). Kinesthetic feedback, such as position and movement of the body in space, and physiological state, such as fluctuations in hormones and neurotransmitters that occur as a result of expectation, stress or circadian rhythms (daily cycles of biological change), can be associated with other stimuli or responses. When this occurs, these internal stimuli become part of the memory retrieval cue package for that response (Roberts, 1998, pp. 121–122, pp. 190–193). This is referred to as state-dependent memory; the inability to retrieve a memory learned in one state when in a different state (Roberts, 1998, p. 190). This is why the dog may be more likely to respond correctly to a cue at a certain time of day, and why antecedent control affects learning.

To avoid association of contextual cues, present the cue in varying contexts. To reactivate a memory that has become dependent on contextual cues, present the cue in the same context (place, time of day, etc.) and practice it there until it is fluent. Ideally, vary external states and variables that impact internal states (such as time of day) individually over time.

If the behavior is not yet fluent, it may require warm-up. Provide the associated reinforcer prior to beginning the session. Rehearse the behavior a few times in the context with which it has a strong association, then immediately move it to a different context. The neurons that support that behavior will be primed by association with the contextual environment and by repetition, and so will be more likely to fire in the new context (Roberts, 1998, pp. 182–184). Regular retrieval also strengthens a memory (Roberts, 1998, p. 199).

**Extinction**

Reinforcements that are given indiscriminately, however well intentioned, teach behavior that may subsequently need to be extinguished (Laurence, 2007). For example, giving a dog a treat because he looks “cute,” or laughing at something a dog does that is “cute,” may be reinforcing a behavior that is inappropriate in daily life. Extinction of that behavior later would rely on a strong emotional response of frustration to alter the dog’s expectation (Roberts, 1998, p. 151). Because of this frustration, extinction is an aversive process (O’Heare, 2007, p. 252). In addition, extinction has limitations because it relies on new learning, not forgetting. This is why extinguished behaviors can re-emerge during a phenomenon called spontaneous recovery (Roberts, 1998, p. 146).

**Priming**

Priming parallels Thorndike’s “readiness” principle of learning. When a dog is motivationally prepared to act, he is more likely to perform that behavior and performance of the behavior is satisfying (Lindsay, 2000, p. 237).
Antecedent control is the manipulation of motivational states so that the animal is prepared for specific behaviors (Lindsay, 2000, p. 250).

Antecedent control is effective, in part, due to neural priming. Monoamines regulate neurotransmission between neurons, but only at currently active synapses (LeDoux, 2002, p. 314). Monoamines magnify the cellular response, encouraging learning of the event that activated that particular set of synapses (LeDoux, 2002, p. 314). Neuromodulators, such as monoamines, affect the resting state of neurons, and therefore either facilitate or inhibit an action potential (Norden, 2007, Part 1, p. 145).

Behavior, and stimulus–stimulus and stimulus–response associations, are a result of the firing of networks of neurons. Networks of neurons that fire together are primed to fire together again. Antecedent control causes physiological changes that prime specific networks of neurons, increasing the probability of specific behaviors.

Neural circuits that support particular behaviors can be primed by antecedent control (Ratey, 2001, p. 161). In addition, undesirable behaviors can be avoided by avoiding antecedents that precede the undesirable behavior, or by changing these antecedents to elicit desired alternative behaviors (O’Heare, 2007, p. 278). For example, counterconditioning can be used to elicit joyful or relaxation responses in the presence of a stimulus that previously elicited fear or anxiety (O’Heare, 2007, p. 281).

Three basic categories of antecedent control are setting events, establishing operations and discriminative stimuli (O’Heare, 2007, p. 235).

**Setting Events**

Setting events, which can occur some time before the behavior, set the context for the behavior, making it more or less likely to occur (O’Heare, 2007, pp. 235–236). For example, stressors such as loud noise, even hours before training, may change the dog’s physiological state so that he is more likely to react aggressively to physical prompting or other annoying events. Dogs deficient in serotonin may be prone to aggressive behavior. Aerobic exercise and supplementing the diet with 5-hydroxytryptophan (5-HTP), which is the precursor to serotonin, can increase serotonin, reducing the likelihood of aggressive behavior (O’Heare, 2007, p. 276).

**Motivating Operations**

Motivating operations cause reinforcers to become more or less valuable (O’Heare, 2007, p. 236). Motivating operations can be divided into two categories: abolishing operations and establishing operations. Abolishing operations temporarily decrease the effectiveness of a specific consequence. For example, feeding a dog his full meal before training using food treats as reinforcement will reduce the dog’s motivation to perform the behavior. Establishing operations temporarily increase the effectiveness of a specific consequence. For example, training a hungry dog just before feeding time, and allowing the dog to sample the food treat to initiate the training session, will activate the dog’s behavioral state for feeding, increasing motivation for food (O’Heare, 2007, p. 249).

A CER can become a motivating operation (O’Heare, 2007, p. 277). For example, a dog that has been trained using only positive reinforcement will associate the training context (handler, training area, training equipment such as the leash and clicker) with a joyful emotion, so will be motivated to approach and interact with the handler. A dog that has been trained using punishment, which entails aversion, pain or fear, will associate the training context with fear, so will be motivated to avoid or escape the training environment. A dog trained using both positive reinforcement and punishment will be conflicted between motivation to approach and motivation to avoid or escape.

**Discriminative Stimuli**

Discriminative stimuli are stimuli that, based on a history of reinforcement, allow the animal to predict that a reinforcer is likely to follow a specific behavior (O’Heare, 2007, p. 236). For example, the dog will respond by sitting when the handler says “sit” if that verbal cue has
preceded the sit behavior on previous occasions, and the dog has been reinforced following the sit behavior. If a behavior is likely to occur following presentation of the discriminative stimulus, that behavior is under *stimulus control* (Roberts, 1998, p. 143).

The type of discriminative stimulus used for a specific behavior can affect the dog’s motivation to perform that behavior. Some stimuli belong to a certain behavioral system, and therefore are a better choice as an antecedent for behaviors related to those behavioral systems (Domjan, 2003, p. 108). If the discriminative stimulus is relevant to the behavior, the learning will be better established (Ratey, 2001, p. 166).

The discriminative stimulus used affects the ease of learning the association between the discriminative stimulus and the behavior, and the discriminative stimulus and the reinforcer. For example, different auditory cues can elicit different states of behavior (McConnell, 2002, pp. 53–64):

- Short, repeated sounds (such as steady hand-claps) stimulate activity.
- Single, long, continuous sounds (such as the long, smooth “hooooe” a horse rider might use to slow his horse) stimulate calm behavior.
- Sudden, short bursts of sound stimulate stopping behavior.

The magnitude of the discriminative stimulus can also affect the level of response, due to the level of attention the antecedent receives. For example, a soft clap of the hands may elicit a casual turn of the head toward the handler. A sudden, loud clap of the hands may result in a snap-turn of the head (Lindsay, 2000, p. 209).

If, at the start of training, the discriminative stimulus is a novel stimulus, it is more likely to gain attention and less likely to be overshadowed due to previous associations or learned irrelevance (Lindsay, 2000, p. 275).

**Contiguity**

Timing is critical for most associations. For example, if the dog chases a cat, then returns to the handler, and the handler scruff-shakes him, the dog will associate the cat with an exhilarating chase, and the handler with physical pain. The dog will be drawn to the cat, and repelled from (or conflicted by) the handler.

For a behavior to become operant, the dog must be able to predict what will occur if a specific stimulus is followed by a specific response (Roberts, 1998, p. 133). The start of reinforcement that begins immediately, within 0.5 seconds of the behavior, is more effective than delayed reinforcement. A delay between the response and the reinforcer disrupts learning because an animal can be performing many responses, and it is difficult for the animal to figure out which response earned the reinforcer (Domjan, 2003, p. 146). A marker that acts as a secondary reinforcer, such as a clicker, can be used to improve contiguity between the response and the primary reinforcer.

There are exceptions to the rule of contiguity in associative learning. Some associations may not require close contiguity. For example, taste aversion can be learned if nausea is experienced several hours after consumption (Roberts, 1998, p. 125).

**Reinforcement**

Reinforcement parallels Thorndike’s “effect” and “intensity” principles of learning. Attention is required for a memory to be stored. Reinforcement causes the dog to be attentive. Therefore, a behavior that is reinforced is more likely to be learned. Aspects that affect the effectiveness of the reinforcer include the reinforcement schedule, value of the reinforcer, salience of the reinforcer, contiguity of the reinforcer, and contrast effect due to expectation. In addition, a phenomenon called the *Premack principle* can be used to build behaviors into reinforcers of other behaviors.

**Reinforcement Schedule**

A schedule of reinforcement is a rule that determines how and when a response, or set of responses, will be followed by a reinforcer.
Schedules of reinforcement affect the animal’s expectation levels and perception of reward, as well as the animal’s choice of different response alternatives (Domjan, 2003, p. 162). Continuous reinforcement, where every occurrence of the target behavior is followed by a reinforcer, helps the animal know when it has performed the target behavior and when it has not. Continuous reinforcement is therefore ideal for teaching new behaviors. Intermittent reinforcement, where reinforcement is presented for some occurrences of the behavior but not all, is best for established behaviors because it inoculates the behavior against extinction (Roberts, 1998, pp. 148–151).

**Value and Salience of the Reinforcer**

A reinforcer that is novel or of high value or magnitude, or otherwise salient to the dog, will elicit attention, enhancing learning (Lindsay, 2000, p. 212). This is because a stimulus that is new, surprising, or of biological importance to the dog causes the hippocampus to choose to store the event in long-term memory, and therefore the association will be learned more quickly (Domjan, 2003, p. 117).

If a reinforcer of biological importance, such as food, is presented following a behavior, more neurons are recruited to support that behavior (Jenkins & Merzenich, University of California, San Francisco, cited in Ratey, 2001, pp. 170–171). Many dog trainers are too quick to wean the dog from reinforcement when teaching a new behavior. The physiology of learning, including the role of reinforcement in the learning process, is an important consideration when deciding when and how to move from continuous to intermittent reinforcement schedules. Reinforcement leads to accelerated learning and an increased level of retention (Roberts, 1998, p. 120).

Anticipation of a reinforcer maintains focus and is, in itself, reinforcing. Neurological aspects of anticipation can be used to increase the value and duration of reinforcement. For example, when the dog has performed the desired behavior, mark the behavior and begin the process of delivering the reinforcer immediately, but draw the reinforcement process out. Begin social reinforcement immediately following the click, using reinforcement through voice (“Gooooood dog. What an excellent dog.”) and facial expression. During this reinforcement, gradually move your hands toward the food treat pouch. Prolong the offering of the food reinforcer by breaking the tidbit into tiny morsels and hand feeding each piece accompanied by relaxed and pleasant verbal praise (Laurence, 2007).

Food and play are not the only reinforcers available to dog trainers. For social animals such as dogs, social approval and belongingness are reinforcing. Innate behaviors, such as predatory motor patterns (eye–stalk, chase, etc.), are intrinsically reinforcing, and so can be used as primary reinforcers in the form of fetch and tug games (Coppinger & Coppinger, 2001, pp. 202–205).

Certain behaviors naturally belong with a specific type of consequence because of the dog’s evolutionary history (Domjan, 2003, p. 140). The expectation of a specific consequence can elicit specific species-typical responses. For example, expectation of food may elicit chewing or licking responses, and expectation of fast movement may elicit stalk-and-chase responses (Domjan, 2003, p. 199). If a stimulus elicits species-specific behavior compatible with the target behavior, learning will occur in fewer repetitions. However, if a stimulus instinctively elicits species-specific behavior incompatible with the target behavior, the stimulus can sabotage training of the target behavior (Domjan, 2003, p. 94). For example, use of a tennis ball to reinforce a sit behavior may instead elicit eye–stalk behavior, particularly in herding breeds. The dog may freeze and stare, rather than sit. Therefore, choosing a reinforcer that is relevant to the behavior supports learning (Ratey, 2001, p. 166).

Because of this, dog sports that require fast running are best reinforced with a stimulus that elicits a chase sequence, such as the fast, jerky movement of a fur-covered tug toy. Alternatively, behaviors such as obedience that require control may be best reinforced with
hand-delivered food reinforcers, which elicit affiliative and consummatory responses.

Attention from the handler is reinforcing for the dog, because it predicts the opportunity to earn reinforcers (Laurence, 2007). However, excitement can be distracting, and therefore can inhibit learning. If a reinforcer generates too much excitement, it may distract the dog from the learning process. The dog may learn a simple task quickly, but may not be able to concentrate on learning a more complex task. When training, be calm during reinforcement. This will keep the dog calm and allow him to learn, rather than distracting him from the learning process (Laurence, 2007).

**Contrast Effect**

Switching reinforcers can affect the behavior, due to contrast effects caused by emotional reactions. If the dog expects a certain value of reinforcer, and a higher value reinforcer is presented, learning will increase because the comparator mechanisms in the dog’s neurological system register a higher than expected reinforcer. This is called a *positive contrast effect*. If a lower value reinforcer is presented, frustration will result that can interfere with learning. This is called *negative contrast effect* (Roberts, 1998, pp. 152–153).

The value and relevance of the expected reinforcer affect the ease of learning. A dog will pay attention when a consequence is relevant (Lindsay, 2000, p. 275). Attention is required for learning to occur, and therefore the type of consequence affects the level of learning. As noted above, if a reinforcer generates a high level of enthusiasm, which could be distracting, a dog may learn a simple task quickly but may not be able to concentrate on learning a more complex task. If a reinforcer is of low value, but high enough to reinforce the response, use of that reinforcer will support learning (Lindsay, 2000, p. 249).

Context also plays a role in reward expectancy. The level of the response can be improved by the context of the situation. (Lindsay, 2000, p. 209) For example, a dog trained to sit for food treats is more likely to have a quick response to “sit” in places where treats have been commonly doled out, such as the kitchen or training area.

The anterior cingulate and orbitofrontal cortex allows the dog to compare the expected result with the actual result (Lindsay, 2000, p. 89; Ratey, 2001, p. 304):

- If the reinforcement is greater than expected, the experience will be surprising and pleasurable, and the behavior will be strengthened. Surprise causes an increase in learning (Roberts, 1998, p. 147).
- If the reinforcement is as expected, the experience will be pleasurable, and the behavior will be strengthened.
- If the value of the reinforcer was overpredicted, the dog will be disappointed, the experience will be aversive, and the behavior will be weakened.

With each consequence, the dog’s expectations shift (Ratey, 2001, p. 304).

**Delivery of the Reinforcer**

Delivery of the reinforcer is an important aspect of learning. Delivery should be planned, so it can be used advantageously in training. For example, food delivered with speed, such as rolling it across the floor, elicits chase. This can increase the value of the reinforcer. Food delivered directly into the dog’s mouth can have a more calming effect. In addition, if food is delivered with verbal praise, the quality and tone of the praise will affect subsequent behavior. For example, excited praise will cause more animated behavior, and calm praise will encourage more calm behavior (Laurence, 2007).

The position of the reinforcer is also an important part of the training plan. After each trial, reinforcer placement can be used to re-set the dog for the next trial. For example, in a “sit” behavior, the food can be placed on the floor one foot in front of the dog, causing him to stand. This positions him to perform another “sit” behavior (Laurence, 2007).
Premack Principle

If a reinforcer is of low value, but high enough to reinforce the response, use of that reinforcer will support learning (Lindsay, 2000, p. 249). Because of this, a response that is more likely to occur can be used to reinforce a response that is less likely to occur (Lindsay, 2000, p. 251). This is the Premack principle.

In dog training, a good example of use of the Premack principle occurs on an agility course. A dog taught to run through an agility tunnel may begin to find this a reinforcing event. The dog can then be taught to weave through a set of weave poles, then upon exiting the weave poles, be cued to run through a tunnel as a reinforcer.

The Premack principle can backfire if it is not well understood. This occurs in behavior chains where a desired behavior is preceded by an undesired behavior, or when a cue is given twice. A cue is an opportunity to earn a reinforcer. Therefore, a cue is, in itself, reinforcing. Cuing a desired behavior after an undesired behavior (or after a failed cue) reinforces not only the desired behavior, but also the undesired behavior (or failed response). For example, if you cue a sit and the dog jumps up, and then sits, you are reinforcing the chain of “jump up, and then sit” (Laurence, 2007).

Repetition

Repetition parallels Thorndike’s “exercise” and “recency” principles of learning. Repetition builds and strengthens the neural connections that support learning (Lindsay, 2000, p. 248). Physiological changes occur when a behavior is repeated, making that behavior more likely to recur.

The motor cortex, with the help of the hippocampus, controls the performance of new motor skill. If a motor skill has been practiced to proficiency, it becomes automatic, and the processes that support it are transferred to subcortical (lower) areas of the brain, such as the striatum, cerebellum and basal ganglia. This frees the motor cortex and hippocampus for other processing (Ratey, 2001, p. 37, p. 157, p. 197). If a behavior has become automatic, it will be more difficult to extinguish. This is why it is important to use antecedent control to prevent the dog from practicing unwanted behaviors.

If the neurons that support a specific behavior are not used, their connections may gradually degrade, leaving that area free to process other behaviors (Ratey, 2001, p. 192). This is the “use it or lose it” concept. This is why it is important to continue to encourage the dog to practice desirable behaviors.

Although repetition is important for learning, a recent study (Meyer et al., 2007) involving dogs indicates that training once per week is more effective than training 5 days per week, when measured by the number of training sessions for behavior acquisition. For practicing a known skill, creating and maintaining muscle tone to support the skill may require practice several times per week. For example, trotting cavalettis to build a proper trotting gait (to avoid pacing) should be practiced 5 minutes per day, 6 days per week, for 3 months (Zink, 2006).

Short training sessions are more effective than long training sessions, since the animal can consolidate learning and return physically and mentally fresh. Short sessions also avoid satiation of the reinforcer, which supports motivation.

In some cases, thinking about performing a behavior causes the same neurons to fire as would fire if the animal performed that behavior. This is called neural mirroring, and occurs when a goal-directed behavior is rehearsed in the mind, such as when an animal watches another animal perform the behavior. Mirroring primes the brain to perform the behavior, because it stimulates the neurons that would perform, allowing rehearsal of the behavior. Mirroring has been proven in some species of monkey, as well as humans (Ratey, 2001, p. 147; Sylwester, 2002). Whether or not dogs have the capability to mirror, and for which types of behavior, would be a useful study. For example, dogs are social animals, and are masters at interpreting subtle body postures. Perhaps mirroring is one method dogs use to learn the meaning and intent of various body postures in other dogs.
**Taproot Behaviors**

Once a behavior becomes automatic, the memories that support that behavior can be stored for life (Ratey, 2001, p. 157). That is why it is easy to ride a bike as an adult if you rode bikes often as a child, even if you have not practiced in decades. It is also why a behavior that your dog has practiced is difficult to prevent: the behavior may have become so familiar that it is automatically performed in response to certain external or internal stimuli.

High levels of reinforcement, and a long reinforcement history, can be used to create *taproot* behaviors: responses that are so familiar they have become automatic. A practice record for taproot behaviors would look something like Figure 9. The primary (most valuable) behavior is listed in the middle of the practice record, with the secondary behaviors either side, and the tertiary behaviors on the outside (as in Figure 9). For each training session, an “X” is marked on the chart for the practiced behavior. Eventually, the practice record begins to appear as a taproot, with the primary behavior being the strongest, because it has the longest reinforcement history (White, 2005).

![Figure 9: Example of "taproot behaviors" practice record](image)

Taproot behaviors have a strong reinforcement history, with high rates of reinforcement, such that the dog performs them almost as an automatic response on cue and they are generalized to virtually all environments. These behaviors become so familiar that performing them feels comfortable to the dog, so they become intrinsically reinforcing. The dog is likely to choose taproot behaviors in times of social pressure or other stress.

**Methods of Teaching**

Our knowledge of the plasticity of the neurological system can be used to select the most effective method of teaching, to optimize learning. There are several common methods used in dog training to initiate a specific behavior: *physical prompting* (also called *molding* or *modeling*), *luring* and *shaping*. Physical prompting and luring are directed learning, whereas shaping is self-initiated learning. These three methods result in different
neurological responses, and therefore result in different learning.

**Physical Prompting**

Physical prompts, such as pushing the dog’s haunches down to teach him to sit on cue, do not support optimum learning. As muscles practice movement, the neurological network connected to those muscles strengthens (Zink, 2006). When a dog is pushed into position, neurons that control the opposing muscles are activated. In addition, the learning process may be disrupted because the physical pressure of hands on the dog’s body can cause the dog to attend to that pressure, distracting him from the behavior of sitting (Arden, 2007, p. 26).

**Luring**

Luring is a quick way to prompt a behavior, to prepare the dog for repetitions of that behavior. However, the dog may attend to the lure rather than the behavior that is being taught. Because of this, lures should be faded in the first two or three repetitions, to allow the dog to initiate and attend to the behavior rather than the lure (Alexander, 2003, p. 76).

**Shaping**

Self-initiated behavior is more strongly learned than directed behavior, because the animal attends to the initiation of that behavior (Laurence, 2005). This is why *shaping by successive approximations* (shaping) is such a powerful tool. Shaping is a process in which a complex behavior is broken into a simple succession of behaviors that approximate the final behavior. The dog is reinforced for the first approximation of the behavior until he has learned it, then reinforcement is withheld until the dog performs the second approximation of the behavior, and so on until the complex behavior is performed (Roberts, 1998, p. 135). In shaping, the level of frustration should be kept to a minimum by thin-slicing the criteria so that the dog experiences minimal negative contrast effect for each criteria shift. If the dog is not earning a reinforcer every second or two, the criteria are not sliced thinly enough for success.

Dogs that are provided with the opportunity to learn regularly through shaping become more adept at learning; they become a partner in the learning process as they “learn to learn.” Shaping provides very mild amounts of frustration as the dog attempts to identify the behavior that earns the reinforcer. This builds the dog’s coping skills and promotes confidence. Shaping also promotes impulse control because the dog must think before acting, in order to perform the behavior that earns the reinforcer (O’Heare, 2007, p. 343).

Learning exercises the brain, increasing blood capillaries and glial cells that feed the metabolic needs of the neurons (Ratey, 2001, p. 193). Intellectually challenging activities, such as shaping, stimulate neural activity, which creates and strengthens neural connections (Ratey, 2001, p. 43). This builds a more resilient brain (Ratey, 2001, p. 37, p. 364).

**Teaching to Actualize Potential (TAP)**

The neurological system has amazing plasticity, particularly during its formation, but also throughout life. This plasticity has the advantage of allowing the dog to learn behaviors that are functional in his environment. The same plasticity has the disadvantage of allowing the dog to learn behavior that is dysfunctional. This is why effective training plans, which consider the physiology of learning, are so important.

All dogs are born with a genetic package. The environment, which includes learning experiences, can allow the dog to achieve the full potential that his genetic package allows. An understanding of the physiology of the neurological system, which supports the principles of learning, gives us the knowledge to teach the dog in a way that will allow him to actualize his potential.

Actualizing potential relies on optimum learning conditions, which involve antecedent control and *microshaping* (shaping minute muscle movement to build responses of particular muscle groups) to ensure that the dog only practices desirable behaviors, building finished behaviors in layers of minute motor skill. Erroneous behavior is avoided altogether,
to avoid practicing and learning unwanted behavior. This takes more planning for the trainer, but is more effective and humane for the learner (Laurence, 2007). This is called errorless learning.

**Errorless Learning**

Thorndike’s operant conditioning was based on trial and error to build neural connections and form behavior. Errorless learning is an improvement on Thorndike’s methods, allowing neural connections to be built without error, and therefore without the need to unlearn and relearn aspects of the behavior.

Errorless learning takes more effort on the part of the trainer, but makes the process of learning easier for the learner. This method is called the *constructional approach*, because the process constructs the desired repertoires one small slice at a time, rather than eliminating incorrect repertoires (Rosales-Ruiz, 2007, p. 33).

Why go to the effort required for errorless learning? Firstly, if erroneous behavior is learned as part of the overall behavior, each error needs to be removed individually by withholding the click until that error is not presented. This is difficult for the trainer and aversive for the dog. While removing erroneous behavior, other errors may be practiced and reinforced. Secondly, practice of imperfect behavior causes that behavior to re-emerge later, especially under stress (Laurence, 2007). And finally, “correct behavior is not simply what remains when erroneous behavior has been chipped away” (Skinner, 1968, cited in Rosales-Ruiz, 2007, p. 33).

In short, the most solid and fluent behaviors are built through practice of minute layers of perfect behavior. Just as in the formation of a pearl, each fine layer is laid down and solidified, acting as a foundation for the subsequent layer.

Errorless learning is accomplished by creating a training plan that breaks the behavior down into tiny slices of criteria, and setting up the environment in such a way that the learner can only perform each slice of behavior correctly. If the trainer is able to manage all the relevant variables to perfection, learning each slice of the perfect behavior may be attained in just one reinforcement (Rosales-Ruiz, 2007, p. 31).

When the dog performs the slice of behavior perfectly, and that behavior is marked immediately and then reinforced, the networks of neurons that fired when performing that behavior will strengthen and become more likely to fire in response to the same contextual cues. With repetition of the perfect behavior (and only the perfect behavior), more neurons will be recruited into the circuits that support that perfect behavior. With perfect practice, the perfect behavior will become automatic. Under stress, such as in competition, that perfect behavior will prevail, because only the perfect behavior will be associated with the cue.

Starting a young dog with errorless learning provides enormous potential, due to the extensive plasticity of the immature brain. However, applying errorless learning at any age has benefits.

**Building an Errorless Learning Plan**

To build a plan for errorless learning, decide on the end goal: What will the behavior look like? Then take that picture and slice it thinly, into micro-criteria. This is called *microshaping* (Laurence, 2008).

In microshaping, the learning process is considered *at least* as important as the end behavior. The trainer invests time in a skill-building process that requires minimal practice because it practices perfect execution of the behavior. Reinforcement rates in errorless learning are 95 to 100%. Because of this, dogs only practice the perfect behavior, so there is no need to extinguish other behaviors, such as superstitious behavior, that could otherwise be practiced as part of the target behavior. The errorless learning process keeps even the most sensitive dogs enjoying the learning game, and results in very solid behavior (Laurence, 2008).

When shaping for errorless learning, set up the environment for the specific behavior you want. For example, choose a quiet and clean
area free of distractions such as enticing scents, loud or unusual sounds, and movement. Carefully analyze the movement of the behavior, from smallest slice to finished product. Think about the perspective of the dog, and how he will perceive all aspects of this environment. With this understanding, plan where you will place yourself, any objects used for training, the dog and the reinforcer (which will be used to reset the dog to repeat the behavior). In this way, you will set up the dog to perform the thin slice of behavior perfectly each time. Perfect practice makes perfect behavior.

A dancer learns a move as an entire pattern. The pattern includes movement of various parts simultaneously. For example, arm and leg movement are practiced simultaneously. The moves are practiced slowly to ensure they are learned correctly. That way, the moves become a single event and are never disjoint. Therefore, when breaking down criteria for a behavior, the thin slices of behavior should include the muscle groups that will be moving simultaneously. This allows the groups of muscles to work together to form an automatic response that includes movement of the entire group of muscles (Laurence, 2007).

Muscles that are not accustomed to performing a specific function will tire quickly. In addition, a brain that is performing a new function will tire quickly as it runs out of fuel stores. Watch the dog for muscle fatigue and keep practice sessions short when teaching a new skill. Ten 1-minute sessions are better than one 10-minute session (Laurence, 2007).

It takes time and practice to build muscle and synapses. Don’t move to the next criteria level until the current level is 90–100% fluent. That is, the dog performs the behavior immediately and correctly 9 out of 10 times, over a period of three training sessions.

Add the final cue (verbal, physical or object) only when the behavior is finished and fluent. That way, the cue will prompt the finished behavior, rather than a previous version, or incomplete, behavior (Laurence, 2007).

When adding a cue, be aware of every movement you are making. Are all the movements part of the cue? Minimize what is not part of the cue, so the dog becomes aware of the cue. Once the cue is learned, vary what is not part of the cue to generalize the cue (Laurence, 2007).

Remember the “readiness” principle. Don’t give a cue unless the dog is ready and able to perform the behavior.

Be consistent with your criteria. Only click a behavior if it has been cued and meets the full criteria (Laurence, 2007). For example, if the dog is barking while he is backing, and barking is not part of the “backing” behavior, then don’t reinforce that behavior.

An Example of Errorless Learning

An example of errorless learning would be teaching trotting heelwork as follows (Laurence, 2007):

1. Stand still and reinforce the dog in the heel position. Set up the environment so the dog is likely to remain in heel position, rather than building a chain of standing in the wrong position, then moving to the correct position. Deliver the reinforcer in a way, and at a rate high enough, that encourages the dog to remain in a perfectly straight heel position.

2. Concurrently, but during separate training sessions, teach the dog to trot in a circle following a target stick (where the target stick was taught previously).

3. Once both behaviors are on cue and have become practiced to proficiency, so that they are automatic and self reinforcing, combine them. The dog can now trot in heel position. This combination of simultaneous behaviors can now be put on a new cue.

Conclusion

Learning and memory make each of us, and each of our dogs, a unique individual. Synaptic connectivity is the essence of learning and memory (LeDoux, 2002, p.134). This connectivity is a result of external and internal stimuli on the genes that create the proteins that
make up our neurological system, and it is formed and re-formed to varying degrees throughout life.

Learning is an important skill for survival and quality of life. Dog training professionals who understand the factors involved in learning will be better skilled at formulating training plans for specific behaviors.

The two most commonly used types of learning in dog training applications are respondent conditioning and operant conditioning. Respondent conditioning, particularly in the form of counterconditioning fear, is a useful behavior modification tool. Respondent conditioning also provides the ability to use a secondary reinforcer as a marker, such as in clicker training. Operant conditioning teaches dogs that they can control their environment by performing certain behaviors.

Learning theory is underpinned by the physiology of the neurological system. The plasticity of the neurological system provides the foundation for lifelong learning. Memory is information that is encoded in the firing or nonfiring, increasing of firing rate or decreasing of firing rate, of neurons. Firing can be modulated or modified by the type of neurotransmitter, increasing or decreasing the amount of neurotransmitter released, modulation of neurotransmission by neuromodulators, and the presence of enzymes that remove neurotransmitters from the cerebral fluid (Norden, 2007, Part 3, p. 36). Simultaneous firing of networked neurons provides the basis for associative learning. The dog’s neurological system changes structurally and molecularly in response to experience (Norden, 2007, Part 3, p. 37). Physiological changes occur as a result of learning, particularly during formative stages, but also throughout an animal’s life.

Learning applies not only to the dog, but also to the handler. Dog training takes mechanical skill. The skills to be used should be practiced by the trainer before introducing the dog—in particular, the three core skills: observation, timing and decision making.

The brain is a complex system, made up of billions of neurons with thousands of ever-changing synaptic connections, acted on in various ways by mixtures of hormones and transmitters (Ratey, 2001, p. 358). The system functions 24 hours a day, 365 days a year, for the life of the animal. It is astounding that, for the most part, the system works as well as it does.

We, as caretakers of the domestic dog, should take due care of the dog’s neurological system. The dog should be provided with a healthy balance of food, exercise and social interaction. Training, whether formal or informal, should always be enjoyable for the dog.

To allow the dog to reach his full potential, we should “Teach to Actualize Potential” (TAP). To TAP into learning, training plans are created that focus on errorless learning by splitting behaviors into easily achievable slices and practicing each slice to perfection before increasing the criteria by adding the next slice. In this way, behaviors are practiced perfectly, resulting in only perfect behaviors.

References


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