CHAPTER TWO
The Evolution of Cognition

Automatic responses play only a limited role in our behavior because life is not perfectly predictable. If a lifetime of events was perfectly predictable then every animal could be born able to automatically make every response it would ever need to make and cognition would be unnecessary. However, life is not perfectly predictable. To make it possible to respond to unpredicted challenges in the world, an elaborated nervous system evolved that made voluntary action possible. The advantage of voluntary over automatic, involuntary action is that it can be ad hoc. Faced with something unexpected, an animal can craft a response it has never made before. Social creatures face a lifetime of new social experiences that require ad hoc responses. For example, dogs who are allowed on furniture often sit where other family members sit. This is how the author came to share a chair with his golden retriever. So the dog would have to move whenever he wanted to sit down. Across the room was the sliding door to the backyard. The retriever learned that to go out he should touch the door. One day when the author was sitting in their chair, the dog touched the door. The author got up and walked over to the door. Before he could open it, the door ran back and sat in the chair.

Cognition begins with the control of voluntary action. In this chapter we will see that cognition evolved to make it possible for an animal to perform novel actions in response to novel, hence unexpected events:

- To make voluntary action possible, at the top of the spinal cord, layer upon layer of representational, computational, and control structure was added, forming brains of increasing complexity, which provided increasingly sophisticated control of voluntary action. The great advantage of a voluntary ad hoc system of action is that it can craft new responses to novel situations, hence respond to change. The great advantage of learning is that successful new actions can be incorporated into future behaviors.

- Voluntary action is synonymous with consciousness. The control of voluntary action is synonymous with cognition.

- Social groups are so effective at dominating their environments that a member's success at raising a family depends more on his or her social standing than any other factor. This is truer of the most social of animals, humans, than of any others. The rapid increase in human cognitive abilities in the past million years occurred to support the social skills that are essential for success. In the last million years humans became smarter and smarter not to outwit plants and other animals but to ingratiate themselves with and sometimes outwit each other.

2.1 <u>Voluntary Action and Learning</u>

The system of unconditioned and conditioned responses is a complex neural systems that supports a sophisticated set of behaviors. Nevertheless, it has two significant limitations. First, reflexes only respond to stimuli as they occur. They cannot react to things in the past or prepare for the future. Second, the domain of stimuli that reflexes may ever respond to is fixed at birth. They do not respond at all to novel conditions outside this domain. To deal with these two limitations, the nervous system evolved three new capabilities, voluntary action, short-term memory, and learning.

Voluntary Action

If every situation an animal may encounter may be predicted at birth then there is no need for it to have the ability to construct new actions. Rather, it may be born with the ability to perform the actions appropriate for the situations it will face. All responses would be automatic. There would be no need for the ability to construct a novel response to an unanticipated situation. There are many creatures whose environments have remained stable over very long periods of time and who have little ability to construct new actions. For example, though insects engage in some complex behaviors, their behaviors are determined at birth.

However, for many creatures life was not perfectly predictable. One cause of unpredictability has always been climate change. Another cause of unpredictability has been the increasing sophistication of inter-species predator – prey relations. As predators became better at tracking prey, the ability to construct novel escape strategies and find novel hiding places to thwart them would be of great advantage to the prey. As prey became better at avoiding predation, the ability to adopt novel hunting strategies and search new locations would be of great advantage to the predators.

Voluntary action evolved to respond to novel situations. The evolution of voluntary action required a large enhancement of the capabilities of the nervous system. The first step towards voluntary action is the ability to construct a representation of the target of the action. This means that the sensory input is used by the brain to construct a mental three-dimensional representation of the world and to describe specific objects in the world. Consequently, animals do not merely detect shapes but see both the animate and inanimate objects in their surroundings. Furthermore, they can hear sounds and identify the sounds with the objects making them. The process of using sensory input to construct a representation of the surroundings is called **perception**.

The Cortex. A basic function of cognition is to compute from the sensory input the relationships necessary to represent the animal's world. The mental representation of the world, along with the actions themselves, is the product of cognition. In mammals, and especially in humans, the mental representation of the world is accomplished by the forebrain and especially by the thick outer layer of the forebrain, called the cerebral cortex, which is shown in Figure 2.1. As shown in the figure, the **cortex** has a large surface area, way too large to fit smoothly within the skull, which is why it is crumpled together. The deep folds that result are called **sulci**, and appear in about the same positions for all humans. So, they are conventionally used to partition the cortex into four different functional areas, called **lobes**, as shown in Figure 2.1. The function of the occipital and temporal lobes is to construct the mental representation of the world from the sensory information available to it. They are responsible for perception and recognition.

The second step towards voluntary action is the coordination of a variety of motor movements to direct an action towards a perceived target. A voluntary action is entirely different from a reflex. An animal is born with a fixed set of reflexes that perform an unchanging set of actions. In contrast, an animal is not born with the ability to perform any particular voluntary action but rather the ability to construct ad hoc voluntary actions to perceptual targets as the need for them arises. The task of planning some purposeful action, directed to a perceptual target, then determining all the muscles in the body that must be contracted and relaxed to perform it, as well as the precise temporal sequence of the muscle movements, and then finally to execute and direct them, is computationally intense. Virtually all of the rest of the cortex that is not involved in perception, the frontal and parietal lobes, is involved in planning and executing voluntary actions.

In the mammal brain, the forebrain exploded in size to increase the number and sophistication of the possible computations, hence the detail of the representation of the world and the sophistication of the actions that may be performed in response to it. If we slice the mammalian forebrain in half, the entire back half of the forebrain is involved in processing sensory input, the top part (parietal lobe) for directing action and the bottom part (occipital and temporal lobes) for constructing a representation of the immediate surroundings. Much of the front half of the forebrain, as well as the midbrain, cerebellum, and spinal cord, is involved in planning and executing such an action.

Voluntary action is completely different from conditioning. In conditioning, the environment controls an animal's actions by activating a reflex. For example, when you salivate, you do not choose to salivate. This occurs as the result of an external stimulus. However, when you pour yourself a glass of water and put it to your lips, you chose to perform these voluntary actions. In Pavlov's classic experiment, a bell came to elicit salivation. In contrast, in Skinner's classic experimental paradigm, an animal is given the opportunity to press a bar to obtain bits of food or water. Given this opportunity, an animal will press the bar repeatedly to obtain the reward of food or water. The ability to remember a reward is an example of **learning**. So, learning is entirely different from conditioning. In conditioning, a stimulus *precedes* and elicits an automatic response. In learning, a reward *follows* the voluntary action and increases the probability that it will be performed again. Learning has been called **operant conditioning**. When this is done, conditioning is called **classical conditioning or Pavlovian conditioning**. Since these terms are not descriptive and imply a false similarity between conditioning and learning, here conditioning will continue to be called conditioning and learning will be called learning.

Consciousness. Another name for voluntary action is **consciousness**. To see why this is so, consider if you consider an action you performed while unconscious as voluntary. Of course, you would not. In order for the action to voluntary, it would have to be accompanied by an intention to act and without consciousness there could not be such an intention. So, at a minimum, voluntary action implies consciousness. However, does consciousness imply voluntary action? What about when a person is lying still, awake, and so perceives the surrounding environment? In fact, as described in Chapter 3, seeing and hearing require the mental actions of looking and listening, which involve exactly the same neural mechanisms of voluntary motor actions except that fewer (or no) muscles are ultimately moved. So consciousness implies (sometimes mental) voluntary action and consciousness and voluntary action are two names for the same thing.

Behavior. Animals do not perform individual voluntary actions independently of one another but sequences of related actions towards a common purpose such as foraging, hunting, or feeding. Such a sequence of actions constitute a **behavior**. One behavior that may be a sequence of voluntary actions is when an animal builds its home. Rats build a complex maze of tunnels and burrows underground. Of course they have no trouble navigating the tunnels they live in, which raises the issue of how rats, and indeed all animals, including humans, find their way around. The study of how rats learn their way through mazes has been a productive area of research in the study of how animals learn to navigate through their environments for over 100 years. It has provided a deep insight into the more general question of how animals learn.

Place versus Response Learning

For over 100 years psychologists have been providing rats with the opportunity to run through mazes to obtain rewards. This is a task that the rat is well suited for and if the reward is consistently hid in the same place then the rat soon learns where to find it. The question is, what does the rat learn when it learns the maze? One possibility is that the rat learns a sequence of actions that result in reaching, the goal, e.g. left turn, right turn, etc. This is called **response learning**. Another possibility is that the rat forms a mental map of the maze that guides its journey through it. This is called **place learning**. These two alternatives have been salient since the work of Edward Tolman (1932), the great promoter of place learning. Tolman collected considerable evidence of place learning during his career, but there was also always evidence of response learning over the many decades that maze learning was studied. The response versus place learning controversy was finally resolved by Packard and McGaugh (1996), more than 60 years after Tolman's great work. Their experiment resoundingly demonstrated that both place and response learning occur. It led to the determination that the mammalian cognitive system includes two distinct, inter-related, and complementary systems of learning and memory. The **instrumental system** is responsible for place learning, and controls the animal's response early in the training. The hippocampus is a key structure. As shown in Figure 2.2, the hippocampus lies deep within the temporal lobe near the center of the brain. The **habit system** is responsible for response learning and controls the animal's response after extensive practice. The caudate nucleus of the striatum is a key structure (Figure 2.2). As shown in Figure 2.2, the striatum lies deep within the posterior portion of the frontal lobe, close to the hippocampus.

The Experiment. Packard and McGaugh (1996) employed the simplest of mazes: the T-maze. As shown at the top of Figure 2.3 (top), the rat was trained to go down the runway and turn right at the crossbar to obtain the reward. After the rat was trained to do this, the runway was flipped, as shown at the bottom of Figure 2.3 (top). If the rat had learned the location of the reward, then when it reached the crossbar, it would now turn left rather than right. If the rat had learned to turn right to obtain the reward then it would continue to turn right.

As shown at the top of Figure 2.3 (bottom), the result was that after one week of practice, the rats turned left, providing clear evidence for place learning. Packard and McGaugh (1996) investigated this finding further. They had inserted two tiny pipettes into the brains of their rats, one into the caudate nucleus of the striatum and one into the hippocampus. By squirting a small drop of anesthetic down a pipette, they could render either the caudate or hippocampus inactive in an otherwise awake and functioning animal. When the caudate was put to sleep, it had no effect on the rat's performance, indicating that the caudate played no role in the animal's left turn. However, when the hippocampus was put to the sleep, instead of always turning to the left, the rats turned left or right equally often, indicating that they had no idea where to go. So, a functioning hippocampus appeared necessary to remember the place of the reward.

This was only the first half of Packard and McGaugh's (1996) experiment. For other rats, the runway was flipped after two weeks of practice. As shown at the bottom of Figure 2.3 (bottom), in this case, the rats turned right, providing clear evidence of response learning. This time putting the hippocampus to sleep had no effect on performance, indicating that it was not in control of an intact rat's response after two weeks. However, putting the caudate nucleus of the striatum to sleep did affect performance. The rats now turned left instead of right. So, when the caudate was no longer inhibiting it, the hippocampus again took control of the animal's response.

Packard and McGaugh's (1996) results indicated that during the first week of training the rat made a sequence of ad hoc actions to move towards the place of reward that it had marked on the mental map guiding those actions. These actions were controlled by the instrumental system. After two weeks of practice, the rat automatically executed a sequence of actions that in the past had brought it to the place of reward. These actions were controlled by the habit system.

<u>Learning</u>. To summarize, once voluntary action is possible, learning is useful. Voluntary action makes new kinds of actions possible. Learning preserves a record of successful actions so they may employed again when a similar situation arises. Together, the instrumental and habit systems address two issues in learning memory: how to learn something new and how to remember something. Through the use of a mental map the instrumental system makes it possible for you to learn your way to class on the first day of school. Through the encoding of a repeated sequence of actions the habit system makes it possible to effortlessly retrace the route to class for the rest of the school year.

The Instrumental System in the Brain and Initial Learning

The functions and characteristics of the instrumental and habit systems are summarized in Table 2.1. The instrumental system encodes both visual and temporal representations of the world. These include maps of the environment but also descriptions of objects, faces, tunes, everything that can be recognized. Notice that this is because all spatial representations, whether of the environment or of a face, are of the same form: the relationship to each other of a set of points in space. Similarly, a tune is a temporal representation of a set of notes in relationship to each other in time.

<u>Mental Maps.</u> Experiments with rats have shown that the hippocampus is part of the neural system for encoding spatial maps of the environment. **Place cells** in the hippocampus are activated every time an animal returns to the same location (O'Keefe & Dostrovsky, 1971). **Grid cells** in the entorhinal cortex, adjacent to the hippocampus within the temporal cortex, encode the location and position of a rat as it moves from place to place (Stensola, Stensola, Solstad, Froland, Moser, & Moser, 2012) Place and grid cells combine to identify the location of the rat in a mental map (Azizi, Schieferstein, & Cheng, 2014).

The use of a mental map by a rat to find a location is demonstrated by the water maze task. The water maze task is simply a platform just below the surface of the water. A swimming rat can use the platform as a place to rest. We can put a little milk in the water and make it cloudy so that the rat cannot see the platform beneath the water. But once the rat finds the platform and uses it as rest stop, the rat can use its mental map to find it again.

Mental maps are part of the cognitive systems of all mammals, including humans. When you stand at your front door, can you point where your bedroom is? Can you point correctly even with your eyes closed? To perform this task, you are using your mental map. One advantage of a mental map is that you don't have to be able to see something to know where it is. You only need to know where it is on your mental map. Stimulating the entorhinal cortex with a mild electric current while humans played a virtual taxi game in which the goal was drop off passengers as quickly as possible in an unfamiliar city, improved performance on the task. Entorhinal stimulation applied while the subjects learned locations of landmarks enhanced their subsequent memory of these locations: the subjects reached these landmarks more quickly and by shorter routes, as compared with locations learned without stimulation (Suthana, Haneef, Stern, Mukamel, Behnke, Knowlton, & Fried, 2012).

The instrumental system is not restricted to the temporal cortex. The instrumental system extends forward from the medial temporal region of the brain to the prefrontal cortex, which uses place and location information to plan actions, as will be described in Chapter 2.

<u>Reward</u>. Instrumental learning is also influenced by both pleasure and pain, which are possible emotional reactions to the consequence of an action. Positive emotional responses, which are collectively called **rewards**, include various degrees of joy and pleasure, including sexual attraction. At the tip of the caudate is the **nucleus accumbens**, which is the pleasure center of the brain (Feltenstein & See, 2008). When the nucleus accumbens responds to an input, that input is perceived as pleasurable. The nucleus accumbens is strongly activated by food, water, and sex. Unfortunately, it is also strongly activated by amphetamines, cocaine, opiates, and alcohol, thus leading to self-destructive addictive behavior.

Rewards cause instrumental learning, consequently increasing the probability of the action being performed again to the same target (Yin & Knowlton, 2006). Having once enjoyed a car ride, a dog may subsequently leap in when its door is opened. Animals are responsive to changes in reward over time. Animals initially trained on large food rewards work less hard for less food (Justel, Pautassi, & Mustaca, 2014). Animals initially trained on small food rewards work harder for more food (Dwyer, Lydall, & Hayward, 2011). Hence, two groups of animals will respond differently for the same reward if their training rewards have been different.

Pain, also called punishment, also causes instrumental learning. However, pain reduces the probability of an action being performed again in the same context. Any mammal, including a human, is much less likely to again touch a surface that has given them a painful electric shock. As shown in Figure 2.2, the tip of the hippocampus is adjacent to the **amygdala**, which controls a reflexive avoidance response (Chapter 1). When a painful target is encountered, the avoidance response becomes the initial component of a more general emotional response that causes the encoding of the action, target, and context causing it.

Short-term Memory

As mentioned in Chapter 1, animals do not perform individual actions independently of one another. The advantage of voluntary action is that completely novel behaviors may be constructed for different environments. For example, different actions are required to catch birds, mice, and fish. Rather, than having different a single, automatic, hunting behavior, cats can combine different sequences of voluntary actions to prey on almost anything.

For an animal to engage in a behavior that is a sequence of voluntary actions, at each point in the sequence the animal must know what they have done and what they must do next. Both awareness of what was done and what must be done require memory. Without memory, a cat stalking a mouse or bird would forget what it was doing when the prey was out of sight. The next step in the evolution of cognition, the ability to plan a sequence of voluntary actions, makes this possible. The ability to plan ad hoc sequence of actions and remember which action in the sequence has just been performed is often called **short-term memory**. For most behaviors this name is descriptive because the actions constituting the behavior are performed consecutively over an interval measuring minutes or at most hours. An ad hoc sequence of actions necessary to perform a novel task is under the control of the instrumental system.

The Habit System, Distributed Retention, and Long-term Retention

Through practice the habit system encodes the sequence of actions for performing a task and so controls long-term performance of routine tasks. Because the habit system does not encode mental maps, it does not learn the location of an invisible target. When the hippocampus has been rendered inactive, a rat will never learn the location of a hidden platform in the water maze no matter how many times it finds it accidentally while swimming around.

The robustness of the representation formed is determined by the consistency of the reward rather than its magnitude. If every time the same sequence of actions is performed the animal retrieves some small benefit, the robustness of its representation will be strengthened. Furthermore, as was the case for habituation and sensitization, the robustness of the representation is much more influenced by the distribution rather than the number of times a task is performed. Again, distributed trials result in longer retention than massed trials so that the actions necessary to perform routine tasks are not forgotten. This is a basic feature of the nervous system. Through a variety of neural mechanisms, distributed practice, training, or study always causes a more permanent change than massed experience.

The Complementary Functions of the Instrumental and Habit Systems

In the normal functioning of learning and memory the instrumental and habit systems work seamlessly together as part of a single system. The first time you are in a new supermarket, you must remember where you have already been while searching for items on your list. A mental map makes it possible for you to keep track of locations you have already visited. When you return to a familiar store, you retrieve and retrace the steps you made on previous trips to find the items you need.

<u>Win-shift; Win-Stay</u>. These complementary roles of the instrumental and habit systems are revealed by the responses of rats to two different reward schemes when they search a radial

arm maze (8 arms radiating from a central platform) for food. These schemes are called, respectively, the win-shift and win-stay tasks, shown in Figure 2.4. The win-shift task rewards exploratory behavior. On each trial the animal must shift to a new pathway not previously investigated to obtain all of the food. The win-stay task rewards routine behavior. The animal must repeatedly visit the same pathway to obtain all of the food. Packard, Hirsh, and White (1989) trained different rats on the win-shift and win-stay tasks in a radial maze. In the win-shift task, all maze arms contained one reward each day and the rat had to visit each arm just once and then shift to a new arm to obtain all the food. This task requires that the rat remember where he has just been, which is what the hippocampus does. Rats with caudate damage performed normally on this task but rats with hippocampus damage were impaired. In the win-stay task, 4 of the 8 maze arms were illuminated each day and a rat could repeatedly search any one to find a reward. This task requires that the same action be repeated, which is what the caudate does. Rats with caudate damage were impaired on the task but rats with fornix damage performed better than normal rats. As shown in Figure 2.2, the fornix is adjacent to the hippocampus and is also part of the instrumental system.

Episodes. There are not separate representations of an experience in memory, one in the instrumental and another in the habit system. Rather, there is a single representation of an experience, though different features of it are encoded in different areas of the brain. The single representation of an experience in the animal brain, whose construction is initiated by the hippocampus (Iordanova, Good, & Honey, 2011), is called an **episode.** An **episode** consists of voluntary action, the target of the action, the context of the target, and the result of the action. When an episode is retrieved and the action specified is used to achieve the result specified, the action is **intentional**, i.e. it has an intended result. When an action is planned and executed under the control of an episode, the intended result is the **goal** of the action.

Episodes make it possible to act effectively in routine situations. Most of life is routine. In the case of a routine event, the most effective response is to anticipate the event, prepare whatever action was effective last time in advance, and then execute it as the soon as the event is recognized. Predictable events do not require novel voluntary action. Instead, automatic, hence rapid and unconscious, action is more effective. Episodes guide our behavior from the moment we wake up. When you first open your eyes, you do not look around and think to yourself, “Oh, I see that I am home. I guess that a good plan would be to get out of bed and look for the bathroom.” Rather, before you open your eyes you have a strong expectation about where you are and have prepared an action to begin your day. When you open your eyes, you process the visual field around you just enough to confirm your expectation and then execute the prepared action. The expectation and action are both determined by the “waking episode” that both describes and determines the first event in your daily routine. Since most of life is routine, most of cognition involves retrieving from memory each successive episode in one’s daily routine and repeatedly automatically executing a prepared action to an expected target.

Fear. Though most of life is routine, unexpected challenges do occur, intermittently. Therefore, the key to effective action is to anticipate life events and then rapidly determine whether each experience has any unexpected elements. If not, then the prepared action is automatically executed by the habit system. Otherwise, the instrumental system performs an ad hoc modification of the action that takes account of the unexpected elements of the situation. In a familiar store, you walk straight to the item you want. In an unfamiliar store, you begin to explore.

Though both the instrumental and habit systems cooperate in the encoding of episodes, the emotional state of the creature influences what is encoded. Recall that a large reward drives instrumental learning (Yin & Knowlton, 2006). It might seem consistent that a terrifying experience would also drive instrumental learning because both pleasure and fear are emotional experiences. However, the opposite is the case, when fear is generated instrumental learning is inhibited, hence increasing habit learning in the situation (Packard, 2009). Perhaps the reason for this is that if the animal escapes the situation, encoding by the habit system insures long-term retention of the action resulting in the escape.

So, learning is influenced by both the magnitude and the valence of the emotional response. Fear produces robust traces in the habit system. Presumably, the most important things are lethal, hence terror-inducing. So, if an animal escapes a terrifying situation there will be one-trial learning and the animal will not forget that situation nor the action effecting the escape. For example, if you ever fall out of an airplane and manage to survive, you will not forget it. If you survive by pulling the ripcord on your parachute, you will never ever forget to pull your ripcord in the future.

Recall that the hippocampus merges into the amygdala (Figure 2.2). Recall that the amygdala controls avoidance responses, which are composed of avoidance reflexes to threatening, painful, or noxious stimuli. In fact, the amygdala generates fear, anger, and disgust responses to appropriate stimuli in the environment that include the appropriate avoidance responses. A neural center within the amygdala called the **basolateral complex** is the neural mechanism by which the amygdala influences the type of memory formed. The basolateral complex responds to adrenalin, which prepares the body for action and is produced in quantity as part of the response to a terrifying situation. The **basolateral complex** inhibits instrumental learning as part of the fear response, thus increasing the contribution of habit learning to the episode.

2.2 Neural Bases of Learning

Kandel's finding of more than one sub-cellular mechanism contributing to habituation/sensitization in the Aplysia was the beginning of the accumulation of evidence of numerous sub-cellular, cellular, and super-cellular mechanisms that contribute to learning. The work mentioned here is a hint of the many layers of a complex system that is just beginning to be discovered.

Sub-cellular Mechanisms of Learning

Kandel and his colleagues showed in Aplysia that long-term habituation and sensitization were the result of a variety of sub-cellular changes, primarily to the terminals of the pre-synaptic neuron, which changed the amount of neurotransmitter sent across the synapse. Changes in the strength of the signal from the pre-synaptic to the post-synaptic neuron are collectively referred to as **synaptic plasticity**. Figure 2.5 shows a variety of sub-cellular changes that influence learning.

Long-term potentiation (LTP). Neurons are like tiny living batteries. The electrical charge on the inside of the neuron is different from the charge on its surface. Neurons transmit information across their bodies by de-polarizing, that is equalizing or reversing the charge difference between the inside and the outside, so that an electrical charge rolls from one end of the neuron to the other. The larger the change in charge is, the greater the response strength of the neuron. When a series of high frequency stimuli is applied to neurons in the major pathways of the hippocampus, there is a long-term increase in the amplitude of the electrical potential produced by theses neurons in response to subsequent stimuli (Kandel, Schwartz, & Jessell, 2000). For some tasks, learning is associated with a decrease in strength for some neurons associated with response, called **long-term depression (LTD),** perhaps because it contributes to the specificity of the response (Caporale & Dan, 2008).

Change in number of synapses. There may also be a change in the number of synapses between a pair of neurons, including an increase, called **synaptogenesis**, and a decrease, called **synaptic extinction** (Hongpaisan & Alkon, 2007). Conditions similar to those producing LTP and LTD may also change the number of synapses (Rosenkranz, Kacar, & Rothwell, 2007).

Intrinsic excitability. The excitability of a neuron is its probability to respond to an input signal. Changes in excitability have been found in the nervous systems of a variety of animals (Daoudal & Debanne, 2003).

Neuron-Glial interaction. The majority of the cells in mammal brains are non-neuronal cells called glial cells. These cells both interact with neurons to influence synaptic plasticity and even generate signals themselves. For example, glial cells myelinate a neuron's axon, which increases the speed of the neuron's response (Bains & Oliet, 2007; Fields, 2008). Also, glial cells called astrocytes provide neurons with a chemical necessary for a long-term change in response (Suzuki, Stern, Bozdagi, Huntley, Walker, Magistretti, & Alberini, 2011).

Neurogenesis

A key mechanism that supports trace conditioning and learning in mammalian, including human, memory is **neurogenesis**, which includes two processes, proliferation and survival (Shors, 2009). **Proliferation** refers to the fact that new neurons are born every day in various parts of the brain, especially the hippocampus (Eriksson, Perfilieva, Bjork-Eriksson, Alborn, Nordborg, Peterson, & Gage, 1998). Diet, exercise, and rest all influence the number of neurons born in the brain each day. Most of these new neurons die within two weeks but learning a spatial or temporal task increases causes some of the new neurons to **survive** (Gould, Beylin, Tanapat, Reeves, & Shors, 1999). Those new neurons that are incorporated into the neural representation of what has been learned become a permanent part of the nervous system. Unsurprisingly, neurogenesis is particularly prominent in the hippocampus, which is so important for learning. So our brains are of our own making. If you want a bigger brain then you must adopt a healthy life style but also learn something new every day. Ultimately, neurogenesis and synaptogenesis contribute to an increased area of the cortex being devoted to supporting a highly practiced task. We each have a designer-brain and we are the designers. Areas that are associated with knowledge and skill grow in size with expertise. Furthermore, these processes, along with synaptic extinction, may lead to a reorganization of the area controlling the skill.

Just as habituation and sensitization effects last longer with distributed training than with massed training, distributed training results in longer retention of the learned response than does massed training. For example, when rats were trained to find the hidden platform in the water maze task, performance was better two weeks later after distributed training than after massed training. Performance was correlated with the number of new neurons incorporated into the hippocampus (Sisti, Glass, & Shors, 2007).

2.3 Social Organization

Through the cooperation of the instrumental and habit systems, animals get better at what they do. Two kinds of advantages accrue with experience and practice. The first kind of advantage that accrues with experience is the performance advantage that results from practice. The **performance advantage** is the improvement in performance on a motor or perceptual task as the result of practice. For example, the more an infant practices, the more skillful it becomes at walking. The more a student reads, the faster she reads. Such an advantage occurs through the encoding of sequences of action by the habit system that are performed automatically. Notice that improvement in performance on a task does not necessarily imply any memory of having performed the task before. You can walk but do not remember learning to walk.

The second kind of advantage are **associative advantages**, the animal learns what is good and what is bad. For example, after a larger dog attacks a smaller one, the smaller one subsequently expresses fear and runs from the bark or sight of the larger one. Notice that an animal (or person) may have an emotional response to something without having a memory of ever encountering it before. When a larger dog has attacked a smaller dog, for the smaller dog's safety it is only necessary that it runs from the larger dog. In order for this to occur, it is only necessary for the smaller dog to fear the sound and sight of the larger dog at subsequent encounters. It is not necessary for it to remember their first encounter. Therefore, because the smaller dog exhibits fear of the one that attacked it, we cannot assume that it is aware that it has encountered the larger dog before. In general, associative advantages that result from the modification of behavior on the basis of good and bad experiences could occur without any memory of those experiences. You could develop preferences for good things over bad, and for routes that lead to useful locations and avoided dangerous ones without encoding any memory of the experiences producing those preferences. Why then do we have memories of past experiences at all? The cause of event memory is an extremely useful behavior shared by many animals, the desire to live in groups.

Collective Action. Many kinds of animals are social and there are great advantages to living in groups over living alone. A group of animals can collectively perceive more of their environment than any one animal and collective action can be more effective than individual action for attack and defense. Several members of a group can scout a wider area for food and water than a single individual. Furthermore, the perceptual abilities of all group members are available for detecting foe. A group can arrange themselves in a defensive formation with the strongest members facing outward all the way around and the weaker members in the middle. Finally, a minor and temporary injury to a solitary individual can result in a downward spiral, inability to forage, hunger, weakness, and death. A group member may be sustained by other members of the group until it recovers.

The effectiveness of collective action is limited by the ability of the group members to communicate with each other. Once communication begins, a group of animals is no longer just a group but a social organization. Consequently, social animals have signal systems of varying degrees of complexity. More complex signal systems make more sophisticated social structures possible. The larger and more sophisticated the social structure, hence the more elaborate the coordination of action among group members, the more control the social organization exerts over its environment. The more control it collectively exerts over its environment, the less likely any member of the society in good standing is ever going to starve to death or be killed by a predator. Success in life no longer depends on the animal's ability to act effectively in the natural environment on its own but instead on its ability to rise to a protected level in its society. Members of a successful social group are both comrades and rivals. They are comrades in achieving the success of their group but rivals in the distribution of the benefits of that success. In simple social organizations brute individual strength is sufficient to obtain the largest share of the rewards. However, in advanced social organizations it is possible to form alliances so personal physical strength is no longer determinative. Success in obtaining rewards depends not only on the ability to intimidate other members of the group but also on the ability to ingratiate oneself to raise your status among them.

To raise your status, one must have effective responses to the social behavior of family and friends. This requires recognizing them as individuals and remembering everything they have ever done to you and for you and everything you have ever done to them and for them. The ability to recognize someone (or anything) and remember what she (or he or it) has done is called **declarative memory**. This detailed knowledge makes a sophisticated social organization possible. So, declarative learning and memory is central to social skill. Declarative memory evolved because it supported advanced social skills that were beneficial to the member of an advanced social group because they made it possible for an individual to rise to a leadership position. Effective leaders benefited groups from their advanced social skills in two ways. First, through their leadership, group action became more effective so there were more benefits of collective action to distribute. Second, the leader was able to claim the single largest share of the benefits.

Humans are the most social of all animals, as measured by the size and sophistication of their groups, and by far the smartest creatures, as measured by the sizes of the cortex and hippocampus and the sophistication of their cognitive abilities (Shultz & Dunbar, 2010). As human society became more complex, positive feedback between cognitive ability and social organization produced an astounding increase in the cognitive capabilities of humans (Dunbar & Sutcliffe, 2012).

As inter-species competition became less important to the survival of the social group member, evolutionary pressure did not slow, it accelerated. The likelihood that a group member would have progeny became determined by their standing in the social order, which depended on their social skills, which depended on their cognitive abilities. Thus, an accelerating positive feedback loop developed between social skills and cognitive abilities. As social skills became more important, the cognitive abilities on which they depended improved, which led to increased social skills, which further increased their importance. Furthermore, as social skills improved, the group was ever more effective at dominating its environment. Hence, increased cognitive abilities and social skills did not merely benefit the individual but the group as a whole (Dunbar, 2013).

So, the extreme cognitive abilities humans have developed, including self-awareness, personal identity, and the ability to infer the intentions of others, have not been acquired to outwit dogs and cats, but make it possible to either ingratiate oneself or outwit members of one's own species. Indeed, they are for interactions with the most intimate members, including family members, of one's own group. That is why the anthropologist Robin Dunbar (2013) calls this collection of cognitive abilities the Machiavellian mind.

Declarative Memory. So, when you meet someone for the first time, they appear novel and you know that you have not seen them before. However, when you see this person again, they appear familiar and you know that you have seen them before. **Recognition**, the awareness that something has been perceived or done before, is called **declarative learning** or **declarative memory**. Within philosophy, declarative memory is called "**knowing what**" as in knowing what something is. **Recognition** is another word for declarative knowledge.

Declarative knowledge is not only the experience of familiarity, but the knowledge of what something is. When you see a chair, it not only looks familiar, you know what to use it for. This created another form of the performance advantage, the knowledge advantage. Knowledge is used to direct action. For example, the more a person explores their environment, the more complete their mental map and the easier it is to find their way around. The more words that a student can recognize, the more sentences containing them he can comprehend. Declarative knowledge is possible through the integration of the instrumental and habit systems to construct single representation, the episode. An episode containing a chair as a target includes a mental map of its appearance constructed by the instrumental system and identifies its function, something to sit on, through the sequence of actions necessary for sitting constructed by the habit system.

Declarative memory is often contrasted with changes in behavior as the result of experience that do not involve awareness of the past. A kitten may become better and better at swatting a moving object without remembering the hours of practice doing so, just as none of us remembers the practice required in learning how to walk. Such changes in behavior as the result of experience without any accompanying memories of the experience are sometimes called **implicit learning**. When the change is an improvement in the performance of some task, it is called **procedural learning** or **procedural memory**. Procedural memory has a variety of other names. It may be called motor, perceptual, or perceptual-motor skill learning depending on the context. Within philosophy, it is called "**knowing how**" as in knowing how to do something.

2.4 The Invention of Human Language

Over the past million years, the verbal communication abilities of humans rapidly improved. This led to the second striking difference between the brains of humans and of most other animals. As shown in Figure 2.6, the human brain, as are all animal brains, is partitioned into two hemispheres. The left hemisphere controls the right side of the body and the right hemisphere controls the left side of the body. In describing hemispheric control, term for opposite is **contralateral**. The left is contralateral to the right. In nearly all animal species, the functional organization of the two hemispheres is perfectly symmetrical. Whatever function a particular area in the right hemisphere performs for the left side of the body, the corresponding area in the exact same location of the left hemisphere performs for the right side of the body. However, the pressure to rapidly generate many precise speech sounds breaks that symmetry. Shared left and right control of the tongue, lips, and throat would result in slower, coarser movements that would reduce the speed with which distinct speech sounds were produced. So, for nearly all individuals the left hemisphere contains specialized areas for the production and comprehension of speech that do not exist in the right hemisphere. The ability to rapidly generate and comprehend individual speech sounds, hence individual words, made possible the final leap in the development of human cognition.

About 60 thousand years ago there was a human family just like us with one important exception. They did not yet speak the equivalent of a modern human language. Then they invented modern human language and became just like us, our immediate ancestors. Human language was invented once and carried all over the world by the people who spoke it. All languages spoken today are variants of that original language (Fitch, 2010).

The invention of human language led to a profound reorganization of human memory, resulting in an enormous expansion of human abilities. With the invention of language, narrative became possible. With the invention of narrative, planning story-telling, vicarious learning, and the cultural transmission of knowledge all became possible. Once story-telling was established, autobiographical memory and the details of personal identity became possible. Self-awareness, autobiographical recollection emerged in their modern form.

2.5 What is Cognitive Science?

Every science has two components, its subject matter and the descriptive theory that explains it. Beginning with the control action, the content of the study of human cognition has been explored. We conclude by considering what is necessary to explain it.

Cognition requires the processing of information and the human cognitive system may also be called the human information processing system. Information requires a code, content, one or more operations that change the content, and a medium to represent the code. For example, the code for representing binary numbers is ones and zeros, the content is the particular number or number being represented, the operations include addition, subtraction, multiplication, and division, and the medium may be ink on paper, chalk on blackboard, electric charges in a computer memory, etc. Notice that the content within an information processing system represents content outside the system. For example, numbers represent quantities of objects. In the human cognitive system, the medium is the neurons and pathways of the brain and the content is the representation of the world of an individual’s actions in it. Cognitive psychology describes the code used to represent the world, the operations that encode a representation of the world from sensory input, and the operations that direct a person’s actions.

2.6 Summary

The evolution of cognition begins with the control of action. Almost all animals, except for the very simplest, are born with a set of automatic responses to things they will encounter in the world. Such automatic responses are called reflexes. They include effective responses to both threats (a turtle withdrawing into his shell) and opportunities (a bird turning to the song of a potential mate). Automatic responses can be as simple as an eye blink or as complicated as swimming in a pool. To make such automatic responses possible, an elaborate nervous system evolved that responded to stimuli in the environment with effective actions. Today, many creatures, such as birds, live their entire lives being guided by primarily automatic, albeit elaborate, courting, mating, foraging, feeding, and child rearing responses, which is collectively called instinctive behavior. In fact, automatic responses play important roles influencing the behaviors of all animals. In humans the sexual response, hence sexual orientation, is largely automatic; hence uninfluenced by upbringing.

Automatic responses play only a limited, albeit important, role in our behavior because life is not perfectly predictable. If a lifetime of events was perfectly predictable then every animal could be born able to automatically make every response it would ever need to make and cognition would be unnecessary. However, life is not perfectly predictable and there are two challenges to a purely automatic behavioral response. First, environments change, for example through climate change. Old behaviors may not be effective in a new environment. For example, if potential food sources change, unchanging foraging behaviors may no longer be effective and so the creature starves. Second, natural selection guarantees that there will always be new competitors in the inter-species competition for survival. When dealing with a changing, hence inherently unpredictable field of competitors, an instinctive, hence predictable, pattern of behavior is not an asset. For example, if a herbivore always automatically moves to its best food source then a carnivore that it eats it can evolve that automatically moves to the same locations. However, the food source of the carnivore is the herbivore. Being a predictable meal for someone else is not a recipe for survival.

To make it possible to respond to unpredicted challenges in the world, an elaborated nervous system evolved that made voluntary action possible. The advantage of voluntary over automatic, involuntary action is that it can be ad hoc. Faced with something unexpected, an animal can craft a response it has never made before. To be likely to craft an *effective* new response, the animal must be able to perceive their current situation accurately, remember a similar past situation and what action was effective then, and modify the previous action for the current circumstances. Cognition begins with the control of voluntary action. **Cognition** refers to an animal's representation of itself in the world and the computations on that representation that are required for an animal to construct a novel action appropriate to its situation.

Chapters 2 – 4 begin the description of cognition with the description of the control of action. This is the natural place to begin because the neural mechanisms that originally evolved for the control of muscle movements (Chapter 2) were subsequently repurposed for the control of other cognitive tasks. As discussed in Chapter 2, the ability to perform ad hoc actions requires two stages: first planning of the action occurs in the frontal cortex and parietal cortex and then the performance of the action is directed by the sub-cortical structures the basal ganglia and the cerebellum. Skilled action is the result of repeated practice on a task. Practice results in the encoding of sequences of actions in a plan by the habit system. Subsequently, the plan is retrieved by the habit system and the sequence of actions is performed automatically. Chapter 3 and Chapter 4 describe how the control of neural processing by the prefrontal cortex, parietal cortex and basal ganglia was extended from motor actions that move body parts to mental actions that direct perceptual processing by closing gates in the thalamus, through which all perceptual pathways pass. Sophisticated perceptual skills such as face recognition and reading are learned from repeated practice on those tasks. Practice results in the encoding of representations of the perceptual targets and a plan by the habit system in the habit system for a sequence of actions directing processing to locations in the environment containing predicted target features. As long as predicted and observed features match, perception and recognition occurs automatically.

Chapter 5 and Chapter 6 describe the declarative knowledge that is encoded by the perceptual skills described in Chapter 3 and Chapter 4. Chapter 5 describes visual perception and recognition and Chapter 6 describes semantic memory. Semantic, including visual, representations reside in the temporal cortex and adjacent areas of the parietal cortex. As described in Chapter 6, semantic memory is the basis of language. Language involves the production and perception of novel sequences to encode new information, so language processing requires the instrumental system. However, for language processing to be fast it must be predictive and so it requires the habit system as well. Finally, language processing makes use of specialized control centers in the left hemisphere that make it possible for people to intentionally encode a reproduce the complex sequences of speech sounds they hear through verbal rehearsal.

Chapters 7 – 9 describe how human experience is transformed into the declarative knowledge that is the basis of identity and that directs human life. As described in Chapter 7, learning is initially a social experience between infant and caregiver. It begins with the infant’s innate ability to make and understand emotional responses, which makes meaningful social interactions with a caregiver possible. This provides the basis for referential communication and for language learning. Chapter 8 describes how language provides a useful tool for labelling experiences and organizing them in semantic memory. Chapter 9 describes the roles of the instrumental and habit systems in the sophisticated, mature learning system. The purpose of the system is to encode the targets, contexts, and results, of successful actions in semantic memory. So memory may be viewed as the incidental product of action. To this end, events are characterized as novel or familiar and only novel experiences are encoded as unique experiences by unique episodes in semantic memory. The robustness of the episode is determined by the emotional response associated with it. A strong emotional response indicates an important event, which results in a robust representation. Familiar experiences influence semantic memory by increasing the robustness of episodes in semantic memory describing them.

The evolution of prefrontal and parietal control of processing through the instrumental system also makes intentional learning possible. A person can attempt to learn any perceptual sequence or pattern through verbal or visual rehearsal, though for completely novel sequences this is a difficult task that results in a fragile representation of a short sequence. However, the set of perceptual skills described in Chapter 4 may also include mnemonic skills such as rehearsal that direct sequences of actions rapidly associate familiar visual and auditory targets with representations in semantic memory, making possible the elaboration of information in semantic memory.

Chapters 10 – 12 describe the retrieval of declarative knowledge from semantic memory and its use in the construction of autobiographical memory, which provides each person with an identity. The world that people inhabit is a complicated social world in which many social situations are somewhat novel and several different novel actions are possible. So the past is incomplete guide to the future and a person cannot rely on the automatic execution of a previously effective action. Chapter 13 and Chapter 14 describe visual reasoning, verbal reasoning, problem solving, and intelligence, which all describe the construction of novel actions in novel situations. This required the final evolution of the neural system for generating ad hoc actions that first involved for motor action (Chapter 2) and then was extended to perception (Chapter 3), intentional learning (Chapter 9) and intentional recollection (Chapter 11). These tasks, like motor action (Chapter 2) involve two stages: planning and performance. Mental actions initiated by the prefrontal cortex and parietal cortex through the basal ganglia construct semantic representations of the task and a possible solution to the task before a motor action is taken. The application of the ability to solve novel problems, called fluid intelligence, to daily life requires making decisions under uncertainty; one cannot be certain of the course of future events or what the full effects of one’s actions will be. The emotional system plays an important role in the choice among possible actions by making people risk averse.

To recapitulate the evolution of these basic abilities:

- An innate, automatic response system may come to be ineffective in a changing world. The great advantage of a voluntary ad hoc system of action is that it can craft new responses to novel situations, hence respond to change.

- The ability to perform ad hoc voluntary actions makes learning useful. When an ad hoc voluntary action is successful it is encoded so that when the same situation again arises it may be retrieved and executed again. The basic unit of mammalian memory is the episode, which has four components:
    - Target of a voluntary
    - Context of the target
    - Action
    - Consequence (which is called the reward when positive)

- Learning in mammals, including humans, is controlled by two distinct but integrated systems, the instrumental system and the habit system.
    - The instrumental system includes the hippocampus and controls the response during the initial stage of learning. The instrumental system encodes a mental map of the target and context. Instrumental learning is sensitive to the size of the reward.
    - The habit system includes the caudate nucleus of the striatum and encodes a sequence of actions. It controls a practiced response in a familiar situation. That

is, it determines long-term memory for an episode. Habit learning is sensitive to the consistency of the reward.

- Voluntary action is synonymous with consciousness. The control of voluntary action is synonymous with cognition.

- Social groups are so effective at dominating their environments that a member's success at raising a family depends more on his or her social standing than any other factor. This is most true of the most social of animals, humans, than of any others. The rapid increase in human cognitive abilities in the past million years occurred to support the social skills that are essential for success.

2.7 Further Reading

Carruthers, P. & Chamberlain, A. (2000). *Evolution and the Human Mind: Modularity, Language and Meta-Cognition*. Cambridge.

Dunbar, R. I. M. (2005). *The human story: a new history of mankind's evolution*. London: Faber.

Packard, M. G., & McGaugh, J. L. (1996). Inactivation of hippocampus or caudate nucleus with lidocaine differentially affects expression of place versus response learning. *Neurobiology of Learning and Memory, 65*, 65 – 72.

Whiten, A. & Byrne, R. W. (1999). *Machiavellian Intelligence II: Extensions and Evaluations*. Cambridge.

Yin, H. H., & Knowlton, B. J. (2006) The role of the basal ganglia in habit formation. *Nature Reviews Neuroscience 7,* 464-476.

Questions

Is a voluntary action controlled by the organism or an external stimulus?

What role does the instrumental system play in learning?

What role does the habit system play in learning?

What influences the probability that a voluntary action will be made to a target?

What is the definition of consciousness?

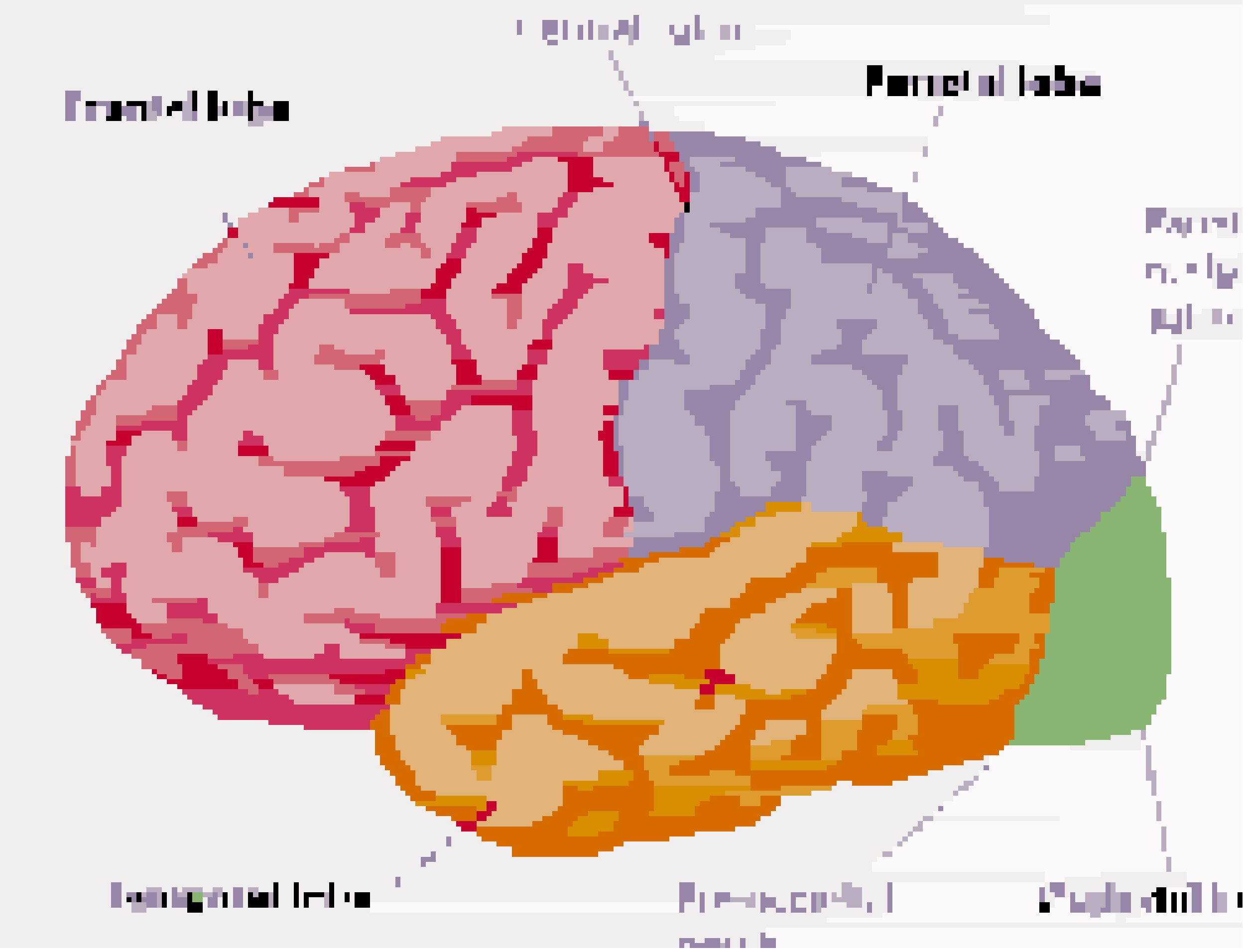
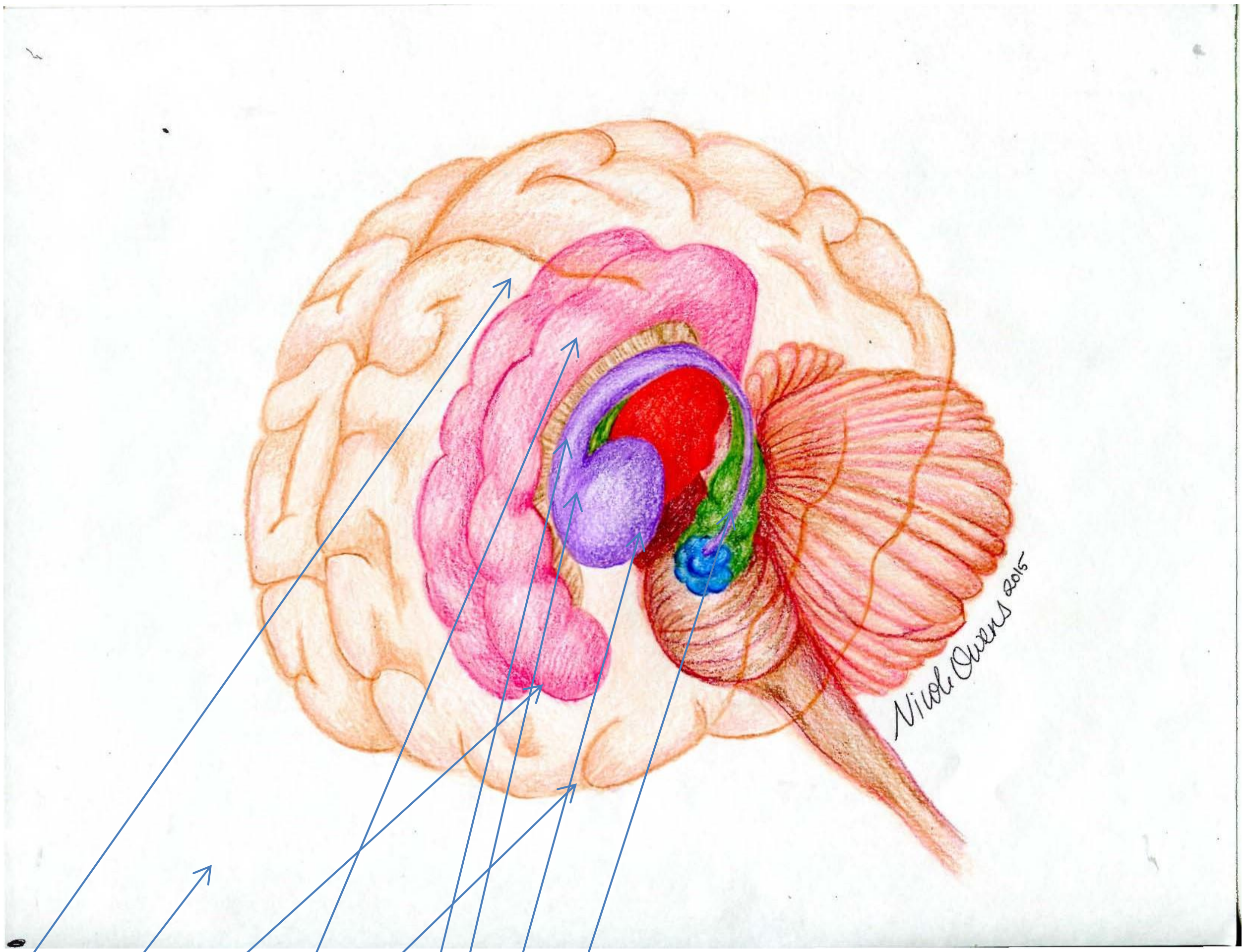


Figure 2.1. The cerebral cortex is conventionally divided into four lobes. The occipital and temporal lobes construct a mental representation of the world. They perform the computations necessary for perception and recognition. The frontal lobe and parietal lobe plan and direct voluntary actions.



Motor cortex; Medial prefrontal cortex; Emotion cortex

Anterior cingulate gyrus; Posterior cingulate gyrus

Nucleus accumbens, Dorsomedial caudate, Dorsomedial putamen, Dorsolateral putamen, Dorsolateral caudate

Thalamus, Anterior nucleus, Pulvinar nucleus, Medial geniculate nucleus

Amygdala, Hippocampus

striatum consists of putamen and caudate

schematic:

Instrumental System:

Medial prefrontal cortex
↓
Dorsomedial striatum
↓
Hippocampus

Habit System:

motor area
↓
dorsolateral striatum

Figure 2.2. The hippocampus is a key structure of the instrumental system and the caudate nucleus of the striatum is a key structure of the habit system.

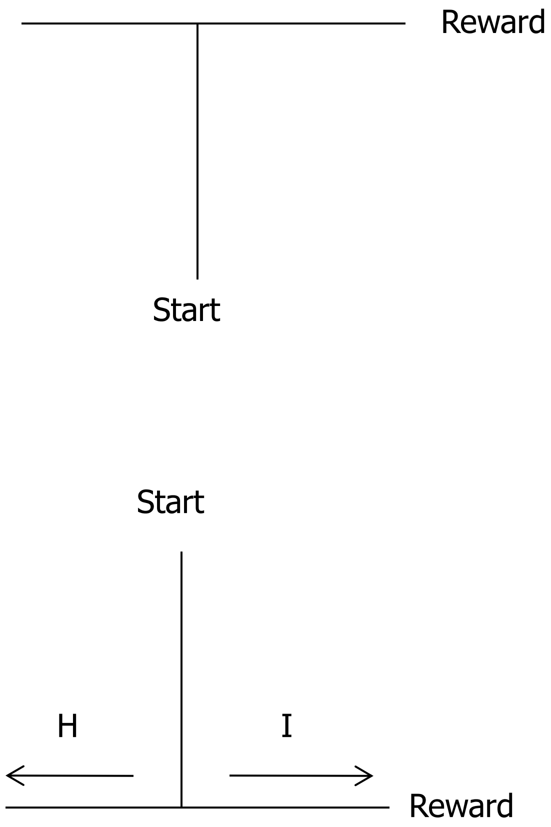


Figure 2.3 (top). Rat is trained to find reward at end of right branch of T – maze (top). Then runway is flipped. If instrumental system controls response, so rat goes to the same place, then rat will now turn left to go to same place. If habit system controls response, so rat makes same response, rat will turn right (bottom).

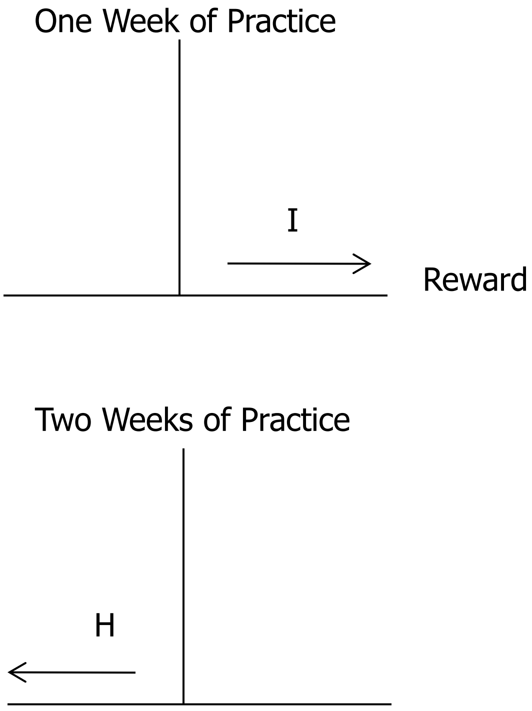
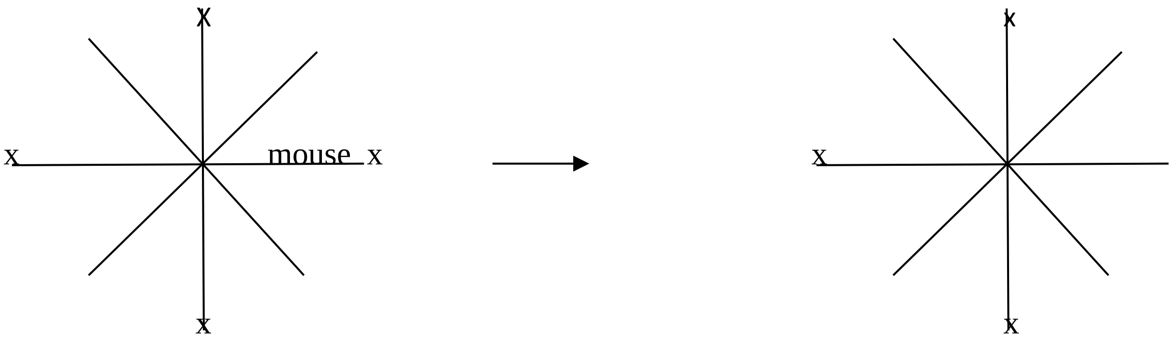
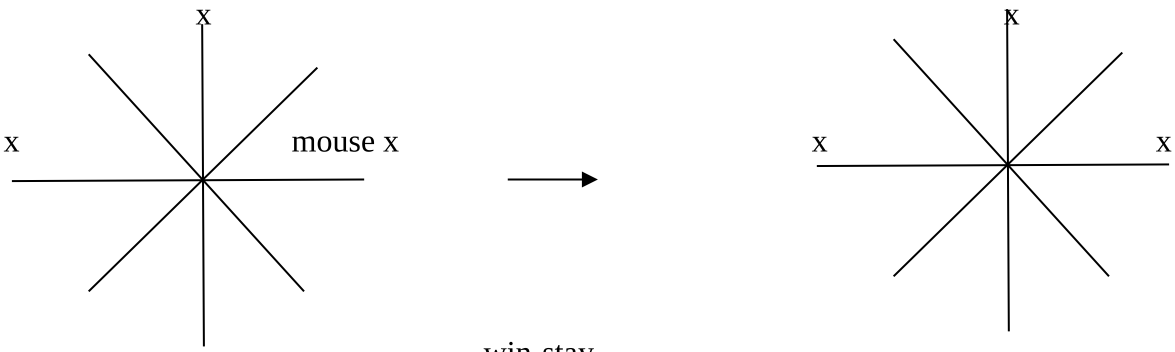


Figure 2.3 (bottom). After one week of training, performance indicates place learning, hence response is controlled by instrumental system (top). After two weeks of training, performance indicates response learning, hence response is controlled by habit system (bottom) Packard and McGaugh (1996).



win-shift



win-stay

Figure 2.4. In the win-shift task, arms of the radial maze containing food are not re-baited so the rat must visit all the arms to find all the food. In the win-stay task, the arms with food are re-baited, so the rat must re-visit those arms where it has found food (Packard, Hirsh, & White, 1989).

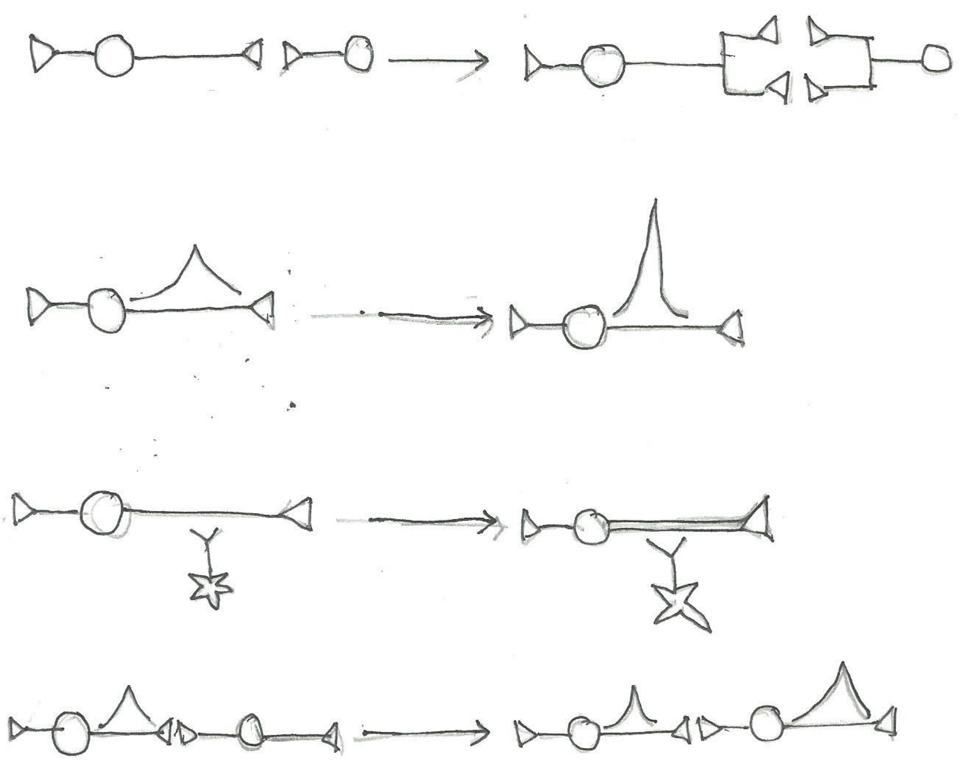


Figure 2.5. A variety of neuronal changes are associated with learning. The number of synapse between neurons may change (top). The size of a neuron's response, called long-term potentiation (LTP) (Kandel, Schwartz, & Jessell, 2000) or long-term depression (LTD) (Caporale & Dan, 2008) may change (second). Glial cells may influence the neuronal response, e.g. they may increase the speed of response by increasing myelination of the neuron's axon (third) (Fields, 2008). The probability of a neuron's response, called intrinsic excitability, may increase (bottom) (Daoudal & Debanne, 2003).

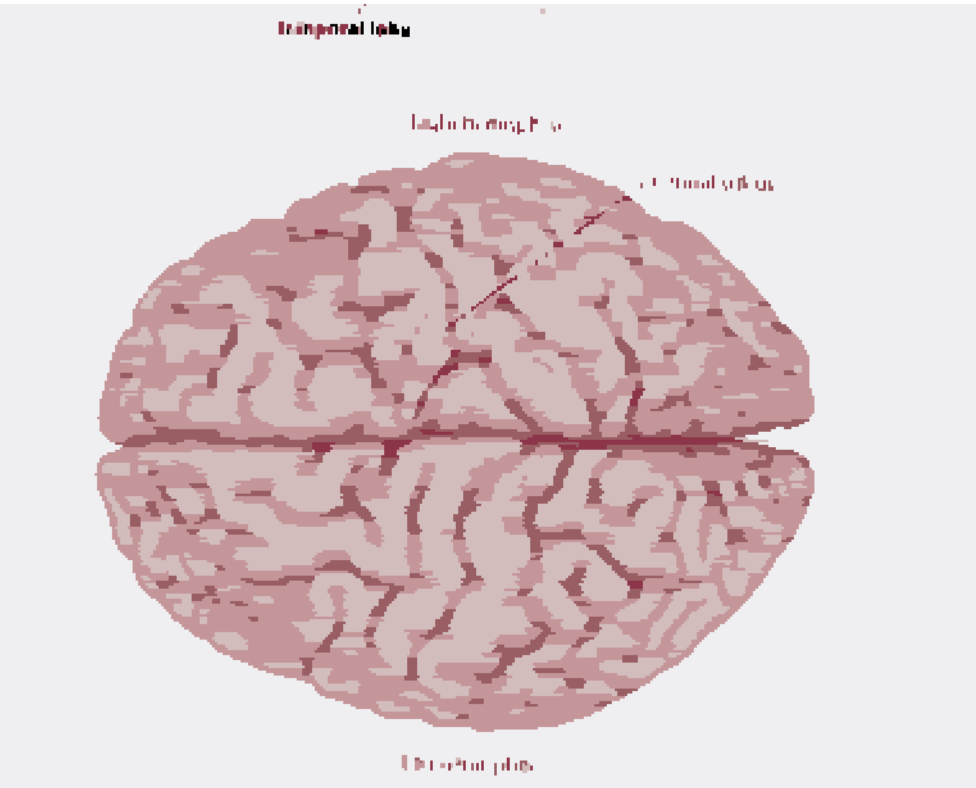


Figure 2.6. The cerebral cortex is divided by the central sulcis into a left and right hemisphere.

Table 2.1

Dual System of Memory (Yin & Knowlton, 2006)

Instrumental System	Habit System
Does not require a visible target	Requires a visible target
Encodes mental map	Encodes a sequence of actions
Influenced by reward magnitude	Influenced by reward consistency
Controls responses during initial learning	Controls responses after extended practice
Requires functional hippocampus	Requires functional striatum