Appendix

Basics of the Nervous System

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<div align="center">**Introduction to the Nervous System**</div>

This text is about the fascinating and often surprising world of our sensory systems and how they operate to allow us the the rich and varied experiences of the world that we enjoy. Much of the operation of sensory systems is also the tail of the operation of the nervous system. A basic knowledge of the structure and operation of the nervous system will be helpful in understanding some of the topics discussed in the main chapters of the text and this appendix will provide the needed background.

So what is the nervous system? The nervous system is the part of our body made up of neurons and their associated support cells. There are, by some estimates, over a 1 billion neurons (REFERENCE) and perhaps over 10 times as many support cells. Collectively, the nervous system controls and coordinates the functions of the rest of the body. As organisms became more complex, there needed to be a way for the organism to be able to have all of its disparate parts function together, for example, move in a common direction. The nervous system evolved to allow the organism to achieve this goal.

<div align="center">**Overview of the Nervous System**</div>

Given the complexity of the human nervous system, it is a wonder that we can understand as much as we already do. Fortunately, the nervous system is highly organized and not a random collection of interconnecting neurons. Without these patterns of organization, the nervous system would probably elude comprehension, and probably would not function as well either. The next few sections will give an overview of the organization of the nervous system.

Overall Organization

The nervous system can be subdivided into several main divisions as shown in Figure AP 1.1. Briefly, the nervous system is divided into two major divisions: the central nervous system (CNS) which is contained within bony cases, in particular the skull and spine, and the peripheral nervous system (PNS) which spreads through the rest of the body. The central nervous system primarily processes information and coordinates the operation of the rest of the body. The peripheral nervous system primarily functions to carry signals to the body from the brain and from the body to the brain. In other words, the peripheral nervous system carries the decisions of the central nervous system to the part of the body to carry out the action and keeps the central nervous system informed of the state of the body and the environment so that the brain can best function.
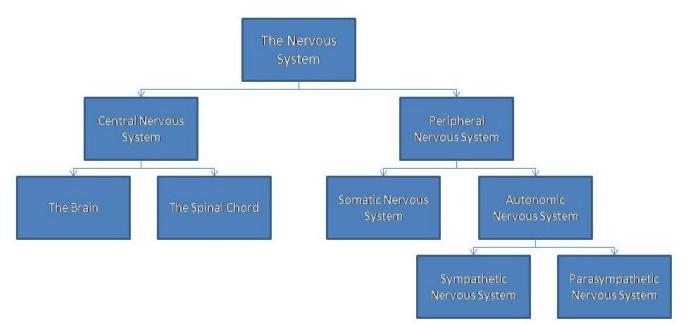

Figure AP 1.1. The major divisions of the nervous system. See the text for details.

The central nervous system can be further divided into two parts, the brain, in the skull, and the spinal chord in the spine. The brain has the great majority of the neurons of the nervous system and primarily functions to process information and is the seat of the most complex processing. The spinal chord dually functions to carry signals to and from the brain and performs many less complicated operations itself.

The peripheral nervous system can also be divided into two further divisions, the somatic and autonomic. The somatic division connects to striated or skeletal muscles. The information coming from the sensory systems is also considered part

of the somatic division of the peripheral nervous system. Sometimes the somatic division is called the voluntary nervous system as it controls the skeletal muscles we can voluntarily move and receives input from the sensory systems that we are consciously attuned to.

The autonomic branch is so called be cause it controls so-called automatic functions such as heart rate and breathing that we do not consciously control. There are two branches of the autonomic nervous system, the sympathetic and parasympathetic. The sympathetic works to increase energy utilization. It is part of the emergency response system of our body. It increases heart rate, breathing and related functions while inhibiting digestion and other systems that impede our emergency responses. The parasympathetic in most cases operates on the same systems but has the opposite effect. For example, it slows heart rate and breathing and stimulates digestion. From these observations one may conclude that the parasympathetic system operates to calm systems and work to increase energy savings. Also, since the parasympathetic system is not nearly as interconnected as the sympathetic system it can help to modulate or adjust the operation of the sympathetic nervous system which tends to operate as a complete system. The parasympathetic nervous system could keep breathing from increasing as much as the heart rate depending upon the situation and in this way allow the operation of the sympathetic system to be more sensitive to particular situations.

With this background, let us look a bit more closely at the brain.

The Brain

Figure AP 1.2 shows the brain in two views, from the side and looking at the middle of a brain that has been cut in half. The brain is a large mushrooming of the nervous system at the top of the spinal chord. The adult brain weighs about 1,300 to 1,400 grams which is a fair about of weight for the delicate spinal chord to carry. To help support and protect the brain, it floats in a sea of cerebro-spinal fluid. The fluid cushions the brain against normal blows to the head that might otherwise cause damage. Additional protection is provided by the skull and three layers of membranes known collectively as the meninges.
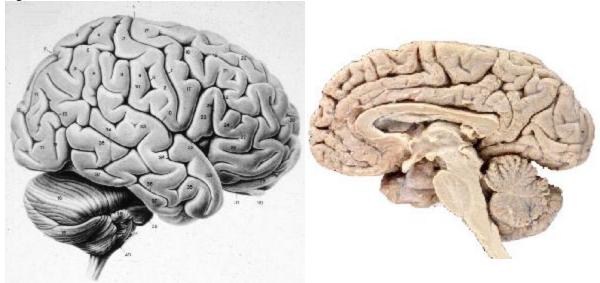

Figure AP 1.2. The Brain. On the left is the view from side. On the right is the view looking at the brain that has been cut in half.

The central nervous system is typically divided into three main regions as shown in Figure AP 1.3. These divisions are derived from studying the development of the brain. Starting at the base of the brain, the hind brain is made up of the medulla, the pons and the cerebellum. The medulla is, in appearance, a swelling of the spinal chord. It is largely tracts of fibers carrying information to and from the rest of the brain. However, there are important centers, called nuclei (or a **nucleus** in singular).   Related to sensation an perception there are centers related to hearing, e.g, the cochlear nucleus, taste, e.g. the nucleus of the solitary tract, and the lemniscal pathways of the somatosensory system. The pons rests above the medulla. Towards the back of the heard from both the medulla and the pons and the medulla is the cerebellum. The cerebellum is a complex figure that seems involved in some forms of learning and in some elements of motor control. Still, we will not run into it in the course of our discussions about sensation and perception, though it would not surprise me if in the future we did not need to know more about this structure.
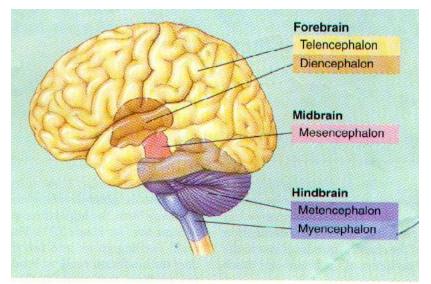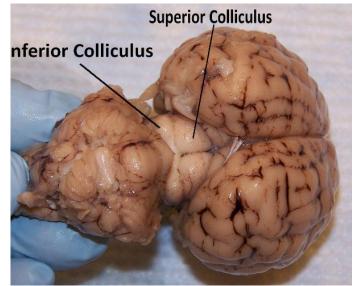
Figure AP 1.3. The three major divisions of the brain.

The midbrain is a very small region of the brain as shown in Figure 1.3. It is made up of two parts, the tectum and tegmentum. The tegmentum plays some important roles in movement. The tectum is divided into two parts the superior colliculus and inferior colliculus. They form two bumps at the back of the brain stem as shown in Figure 1.4. While the midbrain is quite small it these two structures are quite important elements of our sensory systems. The superior colliculus plays a role in the visual system. In fact in animals that lack a forebrain, such as reptiles, amphibians, and birds, the superior colliculus, called the optic tectum in these animals, is the primary visual center in the brain. The inferior colliculus is an important processing center for our auditory systems.

Figurer AP 1.4. The Inferior and Superior Colliculus of the Midbrain.

The Forebrain
Above the midbrain, the brain expands into the forebrain. The forebrain can be divided into several sub-regions. In this section, I will focus on those structures that are most relevant to the sensory systems and their geographical relationship to each other.

The Diencephalon. At the top of the midbrain are three structures that are still considered part of the brain stem (Kolb & Whishaw, 1996). Collectively they are called the diencephalon, and individually they are the hypothalamus, **thalamus**, and

pineal body (Figure AP 1.5). The pineal body plays a role in regulating our daily cycles such as our sleep/wake cycles. The hypothalamus is vital in controlling many of our basic biological functions including eating. In addition, the autonomic system is largely controlled from the hypothalamus. From the perspective of the sensory systems, the thalamus is the most important of these three three structures. The two thalami, one in each hemisphere, are made up of numerous different nuclei, areas for synapses to occur. These different nuclei connect to and receive connections from most regions of the cortex of the forebrain. Our sensory systems all connect with the thalamus prior to proceeding to the cortex. So the visual system connects to the lateral geniculate nucleus of the thalamus before reaching the visual cortex, and the auditory system connects to the medial geniculate nucleus of the thalamus before reaching the cortex.
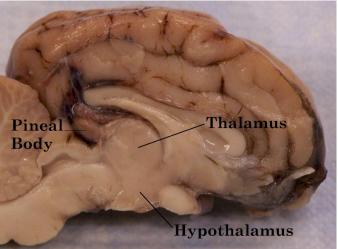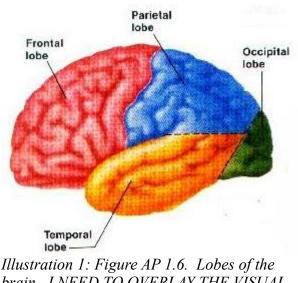

Figure AP 1.5. The Diencephalon showing the hypothalamus, thalamus, and pineal body. WILL WANT A HUMAN BRAIN FOR THE TEXT

The Lobes of the Brain. The forebrain is divided into four general regions of the brain to assist us in knowing where a part of the forebrain is to be found. These lobes are the frontal lobe, in the front of the brain, the temporal lobes on the side, the parietal lobe, found on top, and the occipital found on the back (Figure AP 1.6). These lobes are names after the bones of the skull that they are under.   The top layer of the lobes is the cortex where most of the synaptic connections of the forebrain are to be found. The occipital lobe contains the visual cortex. In fact, the occipital lobe is primarily visual in function. The temporal lobe has the auditory cortex along the top horizontal bump. The somatosensory cortex is in the front of the parietal lobe. Taste and smell are found nearby. Further discussion of the cortex will be saved for later. Now it is time to examine the cells that make up the brain and how they interact with each other.

Illustration 1: Figure AP 1.6. Lobes of the brain. I NEED TO OVERLAY THE VISUAL, AUDITORY, AND SOMATOSENSORY CORTEX ON THIS IMAGE.

The Neuron: Connecting Different parts of the Brain

Structure

The **neuron [to glossary]** is a cell of the body. That may seem a trivial statement but this statement reveals an important feature about theories. The more general the theory the better we like it. That bodies are made of cells is a theory. An incredibly well supported theory and one of the most general theories in biology. It defines the way we look at living organisms. It is not the point of this text, or this appendix for that matter, to discuss cells, but knowing that a neuron is a cell tells us a lot about neurons. They have all the general features of cells: a nucleus, cytoplasm, lysosomes, mitochondria, a cell membrane (since this is an animal cell), and several other common features. Saying that the neuron is a cell says a great deal. Figure AP 1.7 shows a standard cell and some of its parts.
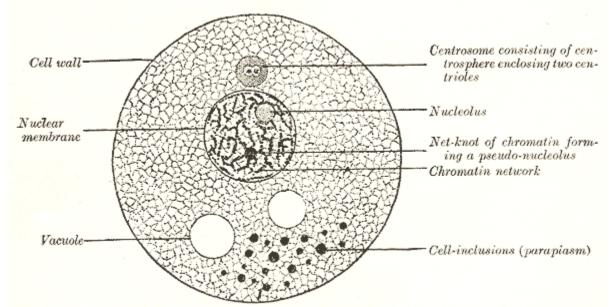

Figure AP 1.7. A diagram of a cell (We need a better image. This is from Grays Anatomy and is not copyrighted but it is dated).

We get so used to what all is being said in such apparently simple statements that we sometimes forget the wonder of it. It was not always certain that the nervous system was like the rest of the body and made up of cells. As recently as the beginning of the 20th century, the debate raged even in Nobel Prize Lectures (GET A REFERENCE).

But, the fact that neurons are cells does not tell us everything. Neurons have several special characteristics that make them different from other cells and function in the ways needed for our nervous system. Figure AP 1.8 shows a standard diagram of a neuron. The additional features of a neuron that are important to note include the **dendrites [to glossary]**, **soma [to glossary]**, **axon [to glossary]** and **terminals [to glossary]**. The dendrites receive information from other neurons. Their function will described below when the synapse is discussed. The soma is the cell body. Soma comes from the Greek word for body. The axon is the part of the neuron that conveys the signal from one location to another. On many axons, there are other cells in the that form an insulating layer called myelin. This myelin sheath is important in speeding up communication within the nervous system. The terminals are in close contact with dendrites and somas and are the other part of a synapse. They may also contact muscles or glands.
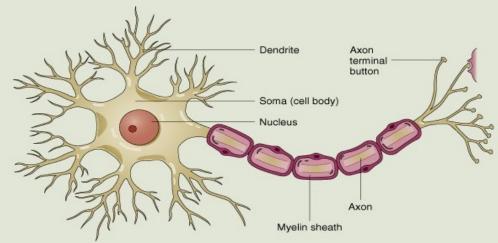

Figure AP 1.8. A standard diagram of a neuron.

Function

The neuron are hard working units of the brain. To function, the neurons require a great deal of energy to function, much of this energy comes from the food that we eat on a daily basis. To expend energy requires that the system store energy to be able to release it. Just as a flashlight requires stored energy, in the form of a battery, the neuron must store energy to be able to function. Energy that is stored, that is, available to do work, is called **potential energy** and the energy doing the work is called **kinetic energy**. Kinetic comes from the ancient Greek word for motion as energy doing work often causes motion of some sort and this circumstance will not be an exception. In the neuron, the potential energy is referred to as the **Resting Potential** and the kinetic energy is referred to as the **Action Potential**.

The key to the functioning of both the resting potential and the action potential lies in the cleverly organized cell membrane (Figure AP 1.9). Without going into too much detail, the cell membrane is a phospholipid bi-layer. The phospolipid molecule, show as a ball (the phosphate part) and two sticks (the lipid part) is the key to the membrane. The phosphate part is slightly negatively charged while the lipid part is electrically neutral. The importance of this feature of the molecule comes from the fact that is surrounded by water molecules. A water molecule, while overall electrically neutral, is slightly polarized, or charged, in across its length. The oxygen part of the water molecule is slightly negative and the hydrogen part is slightly positive. Recall that opposite charges attract while negative charges repel and now the formation of the cell membrane is clear. The phosphate part of the phospholipid molecule is drawn towards the hydrogen part of the water molecule which turns the lipid part away from the water molecule. As a result the phosphate head is referred to as hydrophilic or water loving and the lipid tails are called hydrophobic or water scared. The easiest form for the phospholipids to group together to make both parts of the molecules exist in the happiest environment possible is to form a sphere with water inside and outside and for the molecules to be in two layers with the phosphate heads pointed to the inside and the outside of the sphere. In other words, to form a membrane composed of a phospholipid bilayer.
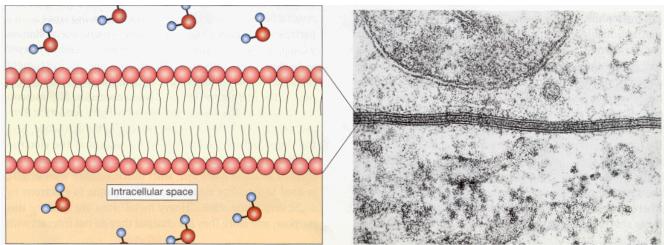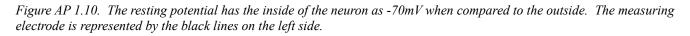
Figure AP 1.9. A diagram of a portion of the cell membrane. The cell membrane is made up of two layers of phospholipids shown by the ball (phosphate part) and two sticks (lipid part). From Smock (1999).

The molecules of the cell membrane are held together by nothing more than these forces. However, this membrane, unmodified, is wholly impenetrable to the small charged particles that are going to be important in the resting potential and the action potential. Therefore, proteins are produced in the cell that are pushed through the membrane, crossing it from one end to the other. These proteins, usually a small group of proteins, form a pore or whole through which small charged particles, called **ions**, can travel. These proteins that allow for ion to cross the cell membrane are called ion channels. With this background, the resting potential can now be described.

DO I WANT TO DO A SEGEMENT ON DIFFUSION AND ELECTRICAL GRADIENTS?

Resting Potential. We will look at the axon during the resting potential in two different ways. First, the electrical of voltage of the resting potential will be described and then the chemical state of the neuron that supports the electrical voltage. The potential energy for electrical energy is measured as voltage. Voltage, like all measures of potential energy, is a relative measure. To measure any voltage you determine its voltage relative to another location, often the earth or ground. To make a voltage measurement of the resting potential, a very fine electrode, called a microelectrode, is inserted into the axon and compared with the reading from an electrode outside the axon. In this case, we measure the voltage of the inside of the neuron compared to the outside of the neuron by convention. During the resting potential, the inside of the neuron is -70 millivolts (mV) or -70 thousandths of a volt (Figure AP 1.10). For a comparison, a AA battery is 1.2 Volts (V).

-70 mV

Figure AP 1.10. The resting potential has the inside of the neuron as -70mV when compared to the outside. The measuring electrode is represented by the black lines on the left side.

Chemically, the resting potential is principally supported by three ions, Sodium, Na+, Potassium, K+, and Chloride, Cl-. Sodium and chloride are found in common table salt, NaCl, held together when solid by their opposite charges. Potassium is a mineral we take in in many foods such as bananas. The majority of the potassium is found inside the neuron while the majority of the sodium and chloride is found outside of the neuron. To help keep the neuron in this resting state, there are more *open* ion channels for potassium than for sodium or chloride. As a result, it is easier for potassium ions to cross the

membrane than for sodium and chloride. The ease for an ion to cross the membrane is called the permeability of the membrane to that ion. The cell membrane is said to be semi-permeable with the greatest permeability to potassium during the resting potential. These ion differences and the semi-permeable nature of the membrane is the major cause for the voltage found during the resting potential.

There is one more feature of the membrane that generates the last remaining bit of the -70 mV resting potential is the **sodium/potassium pump**. The sodium/potassium pump will attach to three sodium ions from inside the neuron and using energy shifts these sodium ions out of the cell. Then two potassium ions from outside the cell attach to the sodium/potassium pump and are brought inside the cell (see Interactive Illustration AP 1.1). The sodium/potassium pump both generates a small part of the resting potential and helps maintain the ionic concentration imbalance for sodium and potassium that are necessary for the functioning of the neuron.

Open Interactive Illustration AP 1.1. When the illustration is opened, you will see a cross section of a neuron membrane going across the screen. Embedded in the membrane is one sodium/potassium pump molecule. The molecules of the membrane are drawn in orange and the blue. The sodium ions will be represented by green squares and the potassium ions will be represented by blue circles. As shown on the screen, the inside of the neuron is below the membrane and the outside of the neuron is above the membrane.

Recall, that in an actual neuron, the majority of the sodium ions are outside the neuron and the majority of the potassium ions are inside the neuron. For illustration purpose, when you start this animation, all of the sodium ions will be inside the neuron and all of the potassium ions will be outside of the neuron. Just remember, this is just for this illustration to show how the sodium/potassium pump works.

Before beginning the animation, look carefully at the sodium/potassium pump. One the left side of the molecule, there are three square wholes in the side. These are the binding sites for the sodium ions. On the right side, there are two curved wholes and these are the binding sites for the potassium ions. Now press the **Start** button to begin the animation and observe the operation of the sodium/potassium pump. A whole collection of sodium ions will start moving around inside the neuron and a whole collection of potassium ions will move around the outside of the neuron. The movement of the ions are random, but the will bounce off of the membrane. At random, a sodium ion or more, will move in the space of the sodium/potassium pump. If the ion gets close enough to the binding site, the ion will become attached to the binding site. When all three sodium binding sites are filled the molecule is ready to change shape and release the sodium out of the neuron. However, to change shape, the molecule needs energy and this energy is provided by the energy storage molecule of cells, adenosine triphosphate or ATP. This energy molecule's role is shown by red **ATP** appearing at the base of the molecule. With this energy, the molecule changes shape so that it is now closed to the inside of the neuron and open to the outside of the neuron. At the same time it releases the sodium ions which can now move to outside the neuron. It is now possible for the potassium ions to move into the molecule. If a potassium ion gets close to the potassium binding sites, they will bind. When both binding sites are filled the molecule will resume its original shape, ATP is not required for this step. The potassium ions are released and the cycle can begin again. As you observe this animation, the amount of sodium outside the neuron and potassium inside the neuron will increase. If you wish to restart the animation, just press the **Start** button and it will restart the animation, though the placement and initial motions of the ions are always random.

A couple of additional points are worth making. The movement of ions are essentially random, and as a result it can sometimes be awhile for the proper ions are bound to the neuron. In our biological systems, it might seem a bit risky to rely on such random processes. Well, there are several changes to the animation that can be made to show how such an apparently random process can work quite reliably. In an actually neuron there will be more ions, more sodium/potassium pumps, and the ions will probably move relatively faster, given the scale of the animation. The controls on the left, **Speed of Ions**, **Number of Sodium Ions**, **Number of Potassium Ions**, **Number of Na/K Pumps**, will allow you to alter the animation in a way to speed up the overall action of the sodium/potassium pump and make the operation appear more regular. When you change the number of sodium or potassium ions, you will need to press the **Start** button again to see the changed number of ions. The other two controls will have their effect as the animation is running. The other point is to recall that during the resting potential there are other channels, particularly for potassium. The sodium/potassium pump restores the balance of sodium and potassium and adjust the actual voltage of the resting potential only a small amount. This pump requires energy and uses a lot of the energy we eat. But without it, the neuron would not work.

Action Potential. The resting potential is the potential energy and the action potential is the kinetic energy of the axon. The action potential can be describe in the same two ways as the resting potential: in terms of the voltage changes on the neuron and also in terms of the chemical events in the neuron and on the membrane. As before, the discussion will start with the description of the electrical changes in the neuron. The action potential is broken down into two main phases and

then some mopping up. In the first phase, the voltage changes, in about 1 msec, from the -70 mV to +30 mV, that is, the inside is now electrically more positive than the outside of the neuron (Figure AP 1.11). This phase is mis-termed the depolarization phase. A true depolarization would be to 0 V as 0 V means that there are no electrical differences between the two sides of the neuron, that is no polarity. Still, the term depolarization has by-and-large stuck. Immediately following the completion of depolarization, the voltage moves back toward the negative voltage and actually the neuron becomes more negative than the -70 mV of the resting potential.   This phase is named the repolarization phase. Not as bad of a name. The overshoot does not last long and the voltage soon returns to the -70 of the resting potential. Overall, the action potential lasts 2-3 msec.
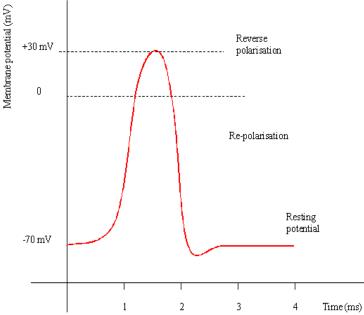

Figure AP 1.11. The action potential. The sweep of the voltage from -70 mV to +30 mV is called the depolarization phase. The change of the voltage back from +30 mV to even more negative than the -70 mV of the resting potential is call the repolarization phase. The period during which the voltage is more negative than -70 mV is sometimes called the overshoot.

The action potential behaves in some rather odd ways. First, action potentials are always the same size. The action potential goes from -70 mV to +30 mV every time, or at least close enough to not matter. Not only that, but the action potential stays the same size as it travels down the axon. Some axons are quite large. There are axons that go from the tip of your toe to the medulla at the base of your brain. These two characteristics of action potentials are termed the **all-or-none law**. This law is curious because in passive electrical systems voltages are easily changes, like the dimmer switch on your lights, and voltages shrink as they travel, thus alternating current is used.

The answer to the oddities of the action potential lies in the events that take place on the neuron membrane. Recall that most of the resting potential happens because of the state of the neuron membrane and the balance of the concentrations of the different ion (sodium, potassium and cloride). The sodium/potassium pump provides a small part of the resting potential voltage but most of the voltage comes from the equilibrium state of the ions and membrane. This equilibrium would hold the voltage about about -67 mV without the sodium/potassium pump (Smock, 1999). A large part of that equilibrium voltage is determined by the permeability of the membrane to the different ions. Recall that it is much easier for potassium to cross the membrane during the resting potential than the other ions. All that changed during the action potential.

Ions need ion channels to cross the membrane. There are more potassium channels open during the resting potential. In addition to these always open channels there are also voltage-dependent ion channels that are normally closed. In particular, there are many sodium and potassium voltage-dependent ion channels that are closed during the resting potential. This situation will change during the action potential.

Open **Interactive Illustration AP 1.2, The Action Potential** to help illustrate the events at the membrane during the action potential. When you open the illustration you will see a membrane running across the top much like Interactive Illustration 1.1, The Sodium/Potassium Pump. However, instead of sodium/potassium pump in the membrane, there are now a series of voltage-dependent sodium (green) and potassium (blue) channels. They are closed at this point so they are drawn as solid

blocks. On the right side there is a recording electrode that records the voltage of the neuron membrane at that point. Towards the bottom of the screen is a graph that will show the voltage detected by the electrode. The resting potential is indicated by a horizontal yellow line. As in the last interactive illustration, sodium ions will be green squares and potassium ions will be blue circles. However, since we are illustrating the action potential, at the beginning of the action potential, the sodium ions will be outside the neuron and the potassium ions will be inside the neuron.

In this illustration, the action potential will move down the membrane from left to right. The voltage at the membrane with during the action potential is color coded with green towards positive voltages and red towards negative voltages. The color of the action potential graph is similarly color coded. When the membrane is at the resting potential, the membrane is drawn in orange so the whole membrane is orange at this moment. In this way you can match up where the action potential is on the membrane with the effects on the ion channels and the voltage being plotted on the action potential graph. With this background, the animation can be played and understood.

Press the **Start** button and watch the animation a first time. When an action potential moves towards the right, the voltage starts moving more positively, shown by the membrane becoming more green, that triggers these sodium ion channels to open which is shown by an opening appearing down the lengths of the green sodium ion channel. Now, much more sodium can cross the membrane. The permeability to sodium has increased. Sodium is positively charged and the inside is negatively charged. Opposite charges attract. So the electrical difference will draw the sodium in. There is much more sodium outside the neuron than inside the neuron so the concentration difference will also lead to more sodium flowing inside the neuron than outside. These sodium ions bring their positive charges inside making the inside of the neuron more positive explaining why, during depolarization, the inside of the neuron becomes more positive. The sodium ions being drawn in by any one ion channel are drawn in yellow to help you distinguish them from the rest of the sodium ions. The question remains as to why the voltage aways stops at +30 mV. Just as the resting potential is largely due to an equilibrium, the opening of the sodium ion channels creates a new equilibrium but with a voltage of +30 mV inside the neuron. The neuron always goes to +30 because that is the voltages new resting state. If these ion channels always stayed open and nothing else changed, the voltage would remain at +30 mV.

So for the voltage inside the neuron to become negatively charged again, several changes in the membrane must occur. The voltage dependent sodium ion channels that opened must close to reduce the permeability of the membrane to sodium back to the level it had during the resting potential. This greatly reduces the travel of sodium across the membrane. In the animation, when the voltage reaches its peak, when the membrane is the brightest green, you will see the sodium ion channel close. In addition, voltage dependent potassium channels open up so that there is more permeability to potassium than even during the resting potential. In the animation, at about the same time, the potassium channel will open and it will begin to draw potassium across the membrane. When a potassium ion is being drawn out of the neuron it will be drawn in cyan. It is this increase in permeability to potassium that causes the voltage to become even more negative than during the resting potential. When these extra potassium channels close and the sodium/potassium pump kicks back in the neuron returns to the resting potential. Of course in the actual neuron there are many more ions and ion channels and the sodium and potassium channels are not attached to each other. They are drawn this way to help in the illustation.

Pressing the **Start** button will restart the animation from the beginning so that you can see how, as the action potential travels down the neuron, you can watch how each sodium ion opens as the action potential reaches it drawing in sodium ions and then closes shortly thereafter. Then the potassium channels open and then close during the overshoot allowing the neuron to return to the resting potential. After the action potential goes completely off of the right side of the screen the animation stops. Notice how there is now an increase of sodium inside the neuron and potassium outside the neuron. If the sodium/potassium pump did not restore the ionic balance to the inside and outside of the neuron you can see how it would become increasingly hard and then impossible to generate an action potential. To help you explore the functioning of the neuron during the action potential there are several additional controls. The **Start** button always restarts the animation, restoring the neuron to its beginning state. The **Stop** button stops the animation in its current position. The **Play/Pause** button will halt and restart the animation from its current place. So you can halt the animation to examine what is going on more closely and then restart it. When paused, the **Step Back (-)** and **Step Forward (+)** button will allow you to move the animation of the action potential a short distance back or forward so you can explore the opening and closing of ion channels in slow motion and under your control. You can also reset the number of ions and the speed of the animation with the sliders on the left side of the screen.

The resulting picture is that the action potential is a wave of opening sodium ion channels that quickly close as potassium ion channels open. This picture of the action potential indicates a limit to how have a neuron can generate action potentials. While one action potential is being generated, it is impossible or harder for the neuron to generate another action potential. This period of time when another action potential is harder or impossible to create is called the **refractory period**. There are two types of refractory periods: **absolute refractory period**, **relative refractory period**. The absolute refractory

period, roughly aligned with the period of time that the sodium ion channels are open, lasts about 1 millisecond. During this time, it is impossible that the neuron cannot generate another action potential.   Doing a simple calculation, it is impossible for a neuron to fire faster than 1000 times a second, though in reality, the fastest neurons are observed to fire is much lower than that. The relative refractory period picks up after the absolute refractory period and during the relative refractory period it is less likely for a neuron to generate another action potential. This lasts 2-3 milliseconds.

This action potential is not an like the way that electricity is conduction in wires at all and as a result is much slower. In an unmyelinated neuron, the action potential travels about 30 m/sec. The role of myelin is to speed up neural conduction along the the axon by reducing the resistance and having the neuron travel under the neuron passively like electricity in the wall allowing it to travel much faster. Passive electricity, recall, loses its voltage as it travels, so the action potential is renewed at the gap between the myelin call Nodes of Ranvier.

<div align="center">The Synapse: Making the Brain Flexible and Learn</div>

The action potential is fixed in invariable. What changes about an action potential on a neuron is how many occur in a given period of time but its characteristics, once fired never changes. Still the brain must be more flexible. It must learn, is must represent all the complex aspects of our perceptions, ideas, emotions, and experience.   While the action potential probably contributes to this experience, there needs to be some feature of the behavior of the brain that shows more complexity than the action potential. The key seems to lie in the synapse. The synapse the place where one neuron comes in contact with another neuron, or sometimes a muscle or a gland. Since the present discussion focusses on the brain, the synapse between two neurons will be discussed, though the synapses between neurons and muscles and glands are similar. First, the structure and then the activity of the synapse will be discussed.

Structure

Figure AP 1.12 shows a diagram of the synapse. First, notice that the two neurons do not tough. That is the most common arrangement. There is a small space between the two cells in the synapse. This gap is called the **synaptic cleft**. This gap is extremely small, on the order of 1 micron (or 1 millionth of a meter). The synaptic cleft is a convenient landmark to use in describing the synapse. Since the synapse is where two neurons connect, we need some language to help keep straight which of the two neurons is being talked about. Fortunately, there is a directional relationship in the synapse. The action potential travels down the axon to the terminal. Then at the synapse this neuron contacts the next neuron in the chain of neural events. So we can talk about the neuron before the synapse, the **presynaptic neuron**, and the neuron after the synapse, the **postsynaptic neuron**.
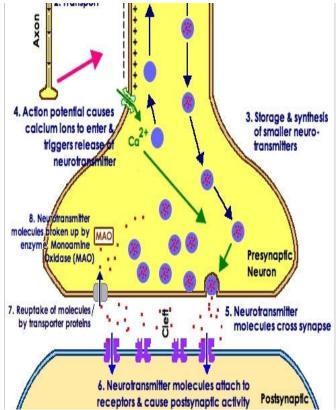
Figure AP 1.12. The structure of a synapse. (I need a simpler figure. Mainly show vesicles, release, and binding.

Before discussing items of the synapse. To understand the reason for all the elements in the synapse, notice the cleft. The action potential has an electrical component to its actions. The cleft looks like a break in the line. The action potential cannot jump even this small break. As a result, the communication between the two neurons cannot be electrical. In this case, it will be chemical.

In the presynaptic neuron, on the top in Figure AP 1.12, there are molecules that that serve the function of the communication between the two neurons. These molecules are called **neurotransmitters**. These molecules are stored in membrane sacks called **synaptic vesicles**. In addition to sodium and potassium voltage dependent ions, the presynaptic terminal has voltage dependent calcium (Ca++) channels. The ability of the terminal to allow calcium to flow into it during an action potential will turn out to be very important in the functioning of the synapse. On the postsynaptic neuron, there are receptor molecules wedged in the membrane. The postsynaptic neuron surface also is embedded with large number of closed ion channels that will be opened by the actions of the synapse.

Function

There are many steps in the operation of the synapse. These steps can be grouped into: preparation, release, binding, removal. Each of these steps will be discussed in turn.

Preparation. The synapse has to be prepared to function just as the axon does. In the synapse, the preparation requires the synthesis and storage of the neurotransmitters. There are many different types of neurotransmitters that have been discovered and depending upon the type of neurotransmitter they process of synthesis is different. Some neurotransmitters are specialized molecules, like acetylcholine, others are modified amino acids like dopamine and serotonin, others are short strings of amino acids, the neuropeptides. Usually the synthesis takes place in the soma so the neurotransmitter must be transmitted to the terminal. Before being released the neurotransmitters must be stored into the synaptic vesicles.

Release. The process of releasing the neurotransmitters into the synaptic cleft begins as an action potential arrives at the terminal. [NEED AN ANIMATION] The action potential has a bit of a different function at the terminal. In addition to allowing sodium ions to enter the axon during depolarization, the terminal also has calcium channels (Ca++). So calcium enters the synapse during action potentials at the terminal. This entrance of calcium is crucial to the operation of the synapse.

To release the neurotransmitters into the synapse, the synaptic vesicles must fuse with the membrane of the terminal. That

is the membrane of the synaptic vesicle must rejoin the membrane that is the wall of the cell. There is a bit of a problem here. As mentioned above when describing the membrane, the outside of membranes are slightly negatively charged. Both the synaptic vesicle and the cell membrane are of the same type of membrane making them both slightly negatively charged and like charges repel. The problem is how to get the two membranes close enough that the can join each other. It is to overcome the mutual repulsion of the membrane that the Ca++ comes in, including its double positive charge. The calcium attaches to binding sites on the membrane and the overall positive charge because of the calcium ion draws the vesicles to the membrane and allow them to fuse, become one membrane again. When the synaptic vesicle membrane fuses with the membrane of the cell, the synaptic vesicle membrane splits emptying its contents into the synaptic cleft. The neurotransmitters have been released (see Figure AP 1.x for now want an animation later).
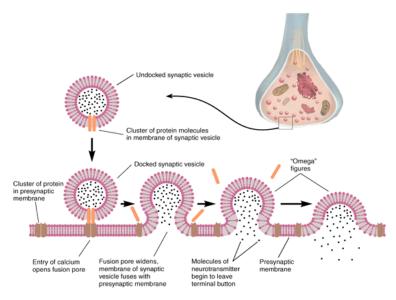
▶ **Release of Neurotransmitter**

Figure AP 1.x. Diagram of the release of neurotransmitters.

Binding. Once in the synaptic cleft, the neurotransmitters move randomly through the cleft. Thousands of molecules are released from each synaptic vesicle so many will bump up against the membrane of the post synaptic neuron. It is also quite likely that they will bump into the receptor molecules that are on the membrane. If there is a shape match between the three dimensional shape of the neurotransmitter and the binding site on the receptor molecule, then the neurotransmitter will bind to the receptor molecule.

But if binding did nothing else, there would be not point is writing about it. The binding of neurotransmitter to receptor molecule leads to events, direct or metabolic, that cause ion channels to open in the postsynaptic neuron membrane. The voltage inside the neuron will change. This change in voltage is called postsynaptic potential (PSP). There are two basic types of postsynaptic potentials, those that make an action potential more likely or less likely on the postsynaptic neuron. The postsynaptic potentials that make an action potential more likely are called **excitatory postsynaptic potentials** (**EPSP**s) and during EPSPs the voltage becomes less negative (Figure AP 1.x). The postsynaptic potentials that make a neuron less likely to fire are called **inhibitory postsynaptic potentials** (**IPSP**s) and make the voltage more negative (Figurer AP 1.x).
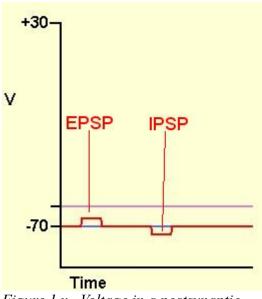
*Figure 1.x. Voltage in a postsynaptic
showing both an EPSP and IPSP.*

Removal. As long as the neurotransmitter remains bound to the receptor molecule, the ion channels will remain open and the postsynaptic potential will continue. So it is important that neurotransmitters do not stay bound to long. Usually the neurotransmitters release after a short time. Still, as long as the neurotransmitter is floating about in the synaptic cleft it could bind again and start a new postsynaptic potential. There needs to be a mechanism to clear the synaptic cleft of neurotransmitter so that the cleft is clear for the next action potential. The neurotransmitters are removed through two processes: destruction and **reuptake**. Destruction occurs because of enzymes that are floating in the synaptic cleft that bind and break apart the neurotransmitter molecules. As a result they no longer have the proper shape and cannot bind. This method of removal is not common for most neurotransmitters. Reuptake occurs when the neurotransmitters actually are reabsorbed into the presynaptic neuron where they can be either destroyed or used again. Most neurotransmitters use this method of removal.

Completing the Circle: Generating a New Action Potential

With synaptic transmission, there remains one more step in the sequence that we have been considering to understand: how does the action potential get started. The discussion started with the action potential already going. Then the function of the synapse was discussed. Now it is time to fill in the missing piece of the puzzle. Open **Interactive Illustration AP 1.x: Spatial and Temporal Summation** which we will use to help bring this concept to life.

When you open the illustration you will see in the main part of the screen will show four neurons drawn schematically with circles for the somas and lines for the actions and angles for the terminals. To simplify this discussion, dendrites are not drawn and the synapses connect right on the soma. Three of the neurons are input or presynaptic neurons, and the neuron of interest is on the right and it is the post synaptic neuron, drawn in gray at the start. The three presynaptic neurons are labelled **A**, **B**, and **C** to help us keep them straight. Two of the presynaptic neurons are drawn in green (**A**, **C**). These neurons generate EPSPs and are excitatory to the post synaptic neuron. The other presynaptic neuron (**B**) is drawn in red and it generates IPSPs and is inhibitory to the postsynaptic neuron. The graph above the above the post synaptic neuron records the voltage at the beginning of the axon on the postsynaptic neuron during animation, including any action potentials. The resting potential is indicated by the yellow line on the graph. The green line on the graph represents a new concept that is important to understand how action potentials are generated. The beginning of the axon is called the axon hillock and it is here that new action potentials are generated. To generate a new action potential the voltage at the axon hillock must reach the voltage represented by the green line which is called the threshold voltage. If the voltage reached the threshold voltage, the action potential will fire, if the voltage does not reach the threshold, then the action potential will not fire.

At this point, let us review postsynaptic potentials. On the left side of the screen are controls for the size, duration and starting time for the postsynaptic potentials to be generated by each of the presynaptic neurons. Each set of controls are labeled by the neuron label (**A**, **B** or **C**). On each neuron it is possible to have two action potentials travel down it and to

generate two postsynaptic potentials each (labeled **First** and **Second** beneath each neuron label). On Neuron **A**, adjust the **Size 1** slider till it equals **4**, which is indicated below the slider. Then press the **Animate** button. An action potential will travel down the **A** neuron and the graph will show the current voltage on the postsynaptic neuron drawn as a cyan (light blue/green) line. When the EPSP from neuron **A** reaches the axon hillock of the postsynaptic neuron, you will see the voltage move up in a more positive direction, but it does not reach the threshold, so no action potential occurs. Return the **Size 1** slider for the **A** neuron to 0 and adjust the **Size 1** slider for the **B** neuron to 4 and again press the **Animate** button. Neuron **B** generates IPSPs so when the postsynaptic potential reaches the axon hillock the voltage becomes more negative.

Summation

It turns out that few if any EPSPs are large enough to reach the postsynaptic neurons threshold, so to cause an action potential. It takes two and often more EPSP. This is the process of **summation**. There are usually thousands of synapses on any one neuron. It is very possible for the postsynaptic potentials to overlap at the axon hillock. The resulting change in voltage is, like the term implies, the combination, like addition, of the postsynaptic potentials present. Two types of summation are talked about, although in most cases, the summation occurring is a combination of the two types.

Spatial Summation refers to the arrival of postsynaptic potentials from different presynaptic neurons. In the interactivity, adjust the **Size 1** slider on **B** back to 0 and put the **Size 1** sliders for both **A** and **C** to 6 and press the **Animate** button. Now when the postsynaptic potentials from both **A** and **C** reach the axon hillock, they are big enough to reach the threshold and an action potential occurs. It is also now possible to understand why IPSPs are truly inhibitory. Leaving the rest of the settings the same, adjust the **Size 1** slider on **B** to 3 and press **Animate**. The two postsynaptic potentials from **A** and **C** used to be big enough to trigger an action potential. Now, however, with the addition of the negative IPSP from **B**, the summed voltage at the axon hillock no longer reaches the threshold and no action potential occurs. It has been inhibited.

Temporal Summation occurs when different postsynaptic potentials from the same presyaptic neuron arrive and add together. Temporal summation occurs because it is quite possible from postsynaptic potentials to last much longer than action potentials. To illustrate this concept return all of the **Size 1** sliders to 0 except for **A**. Leave that intensity at 6. Now use the **Dur 1** slider on **A** and lengthen the first postsynaptic potential to 0.5, indicated below the slider. Adjust the **Size 2** for **A** slider to 6 and press **Animate**. In this case, two action potentials will move down the A neuron. When the first arrives, the postsynaptic potential is visible at the axon hillock but not large enough to cause an action potential. When the second action potential arrives, the second postsynaptic potential shows up that the axon hillock and then the voltage reaches the threshold and the postsynaptic neuron has an action potential.
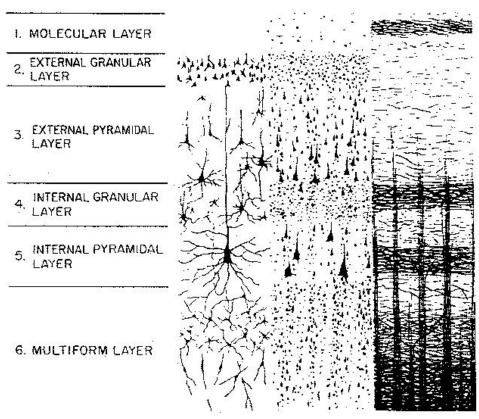
Just a side note. In Chapter 4 the terms spatial and temporal summation were used to refer to the ability to resolve both details and events at different times. It can be confusing to use the same terms for different meanings but, in this case, the use of the terms in Chapter 4 depend upon the use of the terms we have just discussed. Spatial summation in vision is an example of the operation of spatial summation in neurons and the same is true for temporal summation in vision.
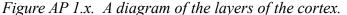
The Cortex

Covering the surface of the cerebrum is the cortex. Depending are the part of cerebrum there are different types of cortex, but most of it is Neocortex which is the most recently evolved cortex. All of the sensory cortices that are discussed in the text are all made up of neocortex. The neocortex is an about 1/4" thick layer that covers all of the primary lobes. The indentations in the brain are all designed to increase the surface area of the cortex. The cortex folds in and out of these indentations on the surface of the brain. In the human brain, the majority of the synapses of the forebrain occur in the cortex. The cortex is so complicated it would be impossible to study without important regularities that allow use to see the organization of the cortex and allow us a means for understanding the functioning of much of the cortex.

Three basic organizational principles will be discussed here. The first is that cortex is organized topographically. That is the cortex surface can be mapped. Think of a map of the earth. Adjacent points on the world are also next to each other on the map. Canada is north of the United States on the Earth, and since north is usually at the top of maps, Canada is just above the United States on a map of the world. That does not mean that maps are perfect. The Earth is roughly a sphere but maps are flat. Inevitably there are distortions. In a normal Mercator projection of the earth, areas near the two poles are greatly over sized on the map. The north and south poles are just points on the Earth but turn into wide areas the same size as the equator on a map. These characteristics of maps are seen in the topographic organization of the brain. In the sensory and motor areas this mapping is clearest. The retina is mapped on the visual cortex. Just as images are upside down and backwards on the retina so they are on our cortex. Just as maps have distortions so does this mapping of the retina on the cortex. The fovea takes up less than 1% of the retina but about 50% of the cortex. Similar types of mapping can be found

for the other sensory and motor areas. The existence of these maps are immensely useful in studying the brain.
The next principle is that the neocortex is organized horizontally into six layers (Figure AP 1.x). Each layer has varies in the type of cells that are found and performs a different function. Layer 1 is at the surface of the brain and Layer 6 is on the inside of the cortex next to the rest of the brain. These layers are the same all over the neocortex and have the same function throughout. What varies is the relative thicknesses of the layers that allows anatomist to identify different regions of the cortex. While each layer has a different function, the layer 4 is the one most relevant to the topic of this text. Layer 4 receives input ultimately from outside the brain. For example, layer 4 of V1 is unusually think as it received the input from the lateral geniculate nucleus. It is the thickness of this layer, which is thicker in V1 than any other region of the brain that leads to one of the names for this later, the striate, or stripped, cortex.
The final organizing principle is that of columns. The columns run at right angles to the layers. The columns run from layer

CEREBRAL CORTEX

Figure AP 1.x. A diagram of the layers of the cortex.

1 to layer 6. The columns were first discovered by Mountcastle (1957). Moutcastle (1957) was studying the somatosensory cortex (see Chapter 12). He found that different areas of the cortex each responded to the different skin senses, for example one region would respond to pressure while the next might respond to temperature. Hubel and Wiesel (1962) refined the concept of columns in the visual cortex finding that different regions of the surface respond to different orientations of the visual stimulus and different eyes. The columns turned out to be carefully organized.

Sensory Coding or How does the Brain able to Let Us Know What is Going on Out There?

To conclude this brief introduction to the nervous system, it seems important to tackle, briefly, one very important topic. In the discussion of the functioning of the neuron, the all-or-none law was discussed. An action potential fires or it does not. Each action potential is essentially the same as every other action potential. This observation begs the question as to how can such a monotonous, boring even, response enable us to experience the rich and varied range of sensory, emotional and cognitive experiences that make up our life. This is the problem of sensory coding. A secret code takes our normal language and translates it into another pattern that ultimately behaves exactly as the language does. The code represents the language completely in a new form. The search for sensory codes is trying to find out how the brain translates the sensory

input it receives into a pattern of activity of the neurons of the brain that in some fashion matches the behavior of the sensory input and how it changes.

A great deal about sensory coding remains to be discovered but some ways that sensory coding is accomplished has be described. Some features of coding depends upon the different operations of a neuron while others use the fact that the brain is made up of many neurons to accomplish the coding. Actual coding uses both the differences in behavior within and between neurons but for simplicity each type of coding will be discussed separately. Open **Interactive Illustration AP 1.x, Sensory Coding** to help illustrate these different coding methods.

<u>**Coding by a single cell**</u>

Some information about the world experience is contained in the cell itself. In fact, one of the the oldest concepts in sensory coding comes from Johannes Müller in the early part of the 19th century who postulated that our experience depends upon which neuron fires. This principle is known as the **Law of Specific Nerve Energies**. Basically, Müller was trying to understand why different regions of the brain yielded such different experience while the brain anatomy looked basically the same in the different regions. He argued that the difference was simply in which neurons were activated. Those neurons in the visual cortex would lead to vision and those in the auditory cortex lead to hearing (REF). Synesthesia supports this concept which is experienced by some people. There are those that report seeing sounds and it is this cross sensory experience that is synesthesia. In this case, auditory stimulation of the visual cortex leads to a visual experience of sound (REF). Dreams also support this concept. When you have a visual experience of dreams, your visual cortex is active (REF). Looking at **Interactive Illustration AP 1.x, Sensory Coding**, use the drop down menu on the left to select **Law of Specific Nerve Energies** which should be selected as it is the default option. Select one of the neurons (**A** or **B**) by checking the **Fire this neuron** next to the desired neuron. The press the **Animate** button. Whichever neuron you have selected will fire. According to the Law of Specific Nerve Energies, the fact that this neuron was firing is what determines your experience. If the other neuron fired, you would get a different experience.

Another means by which a single neuron can code for more than one experience is by its firing rate. This is known as **Frequency Coding**. Frequency coding is found in the auditory system as one of the ways that the brain seems to determine the frequency of the sound. Using the menu on the left select **Frequency Coding**. The arrangement of neurons changes on the screen. There are now three neurons on the left (**A**, **B**, and **C**) that all input into one neuron. There is now a menu above the somas of these three neurons that allows you to **Select Neuron to Fire**. Select first **A** and then **B** and then finally **C** in turn, pressing the **Animate** button after selecting each neuron and observe the results.

As you can see, the number of action potentials generated differs depending upon the input neuron (look to the activity to find out the specifics). So what is being input can be determined by the brain by the firing rate. In Frequency Theory, the pitch of a tone in some cases seem to be determined by the firing rate of neurons (see Chapter 10).

<u>**Coding across many cells**</u>

While individual neurons do seem to provide some information, much more about the world can be learned when a collection neurons are used to allow the coding to distribute itself. This type of coding is known as distributed representation (McClelland & Rumelhart, 1986). Let us take a simple examples of one type of distributed coding, relative firing rate. The cones and their coding of color is a type of example of this type of coding. Even though they do not generate action potentials, their responses fit this type of coding. Each cone class has a different frequency that it prefers to respond to. So for each frequency of light, the strength of responses across the three different cones differ (see Chapter 6 and Interactive Illustration 6.x, Trichromatic Theory). In this way, three cones can help us distinguish thousands of different colors.

To illustrate this means of coding, use the menu on the left of **Interactive Illustration AP 1.x, Sensory Coding** to select **Relative Firing Rate**. There are now six input neurons (**A** through **F**) and three output neurons. Each input neuron is connected to each output neuron. Using the **Select Neuron to Fire** menu, select each input neuron in turn and then press the **Animate** button. Input neuron **A** will only cause output neuron **1** to fire. This outcome is possible because neuron **A** has a stronger connection to output neuron **1** than to the other two output neurons. It generates larger and perhaps a longer EPSP on output neuron **1** than on output neurons **2** and **3**. Still at this point, the outcome seems a bit like the Law of Specific Nerve Energies where which neuron fires is important. But if you look at the figure closely you see that there are 6 input neurons and only three output neurons. If the Law of Specific Nerve Energies operated, there are too few output neurons.

Now select input neuron **B** and press the **Animate** button. Output neuron **1** still fires but it now fires three times and output neuron **2** fires but it only fires once and still output neuron **3** does not fire. Again, this difference in response of the three output neurons is possible because they each have different size and duration EPSPs to the one input neuron (**B**). The

strength of the connection between the input and the output neurons for **A** and **B** leading to a different response of the output neurons. It is not as clear as for the Law of Specific Nerve Energies. It fact it is sort of combination of the Law of Specific Nerve Energies and the Frequency Coding that were discussed above. In fact, as you try each different input neuron you will find that each input neuron generates a different pattern of response on the output neurons. In addition to cones, the response to the basic tastse seem to use this type of coding.

Let us discuss one more type of sensory coding that seems to be used in sensory system. So far, all of the codes have only take advantage of the ability of neurons to generate excitatory connections, EPSPs. It seems unlikely that if neurons can have inhibitory connections, IPSPs, that these connections do not play a role in how we code our sensory systems. In fact, throughout the book several ways that inhibitory connections play a role are discussed. In Chapter 6, the color opponent theory was discussed. For example the long and middle wavelength cones (red and green) input into the Red/Green color opponent cell. If the long wavelength (red) cone input excites the Red/Green cells then the middle wavelength (green) cone inhibits the same cell. If both cones respond equally the Red/Green cell does not respond at all. Use the menu on the left of the illustration to select **Opponent Processes** to see and example of this type coding in action. In this example there are two input cells and two output cells. The input cells connect to both output cells but differently than the last example. Input cell **A** has an excitatory (green) connection to the output cell **1** and an inhibitory connection to output cell **2**. Input cell **B** connects in the opposite fashion to the two output cells. Using the **Select Neuron to Fire** menu you can cause neuron **A** to fire, neuron **B** to fire, and **Both** input neurons to fire. Select each option and press the **Animate** button and see what happens. When neuron **A** fires alone so does output neuron **1** and when neuron **B** fires alone output neuron **2** fires. But when both fire, there is no response by the output neurons. They cancel each other out. This type of coding looks for differences. The response to each neuron alone is emphasized. The response of neither or both seem to be ignored by this type of coding. They lead to the same output: no firing by the output neurons. For example, in out very own color responses, a white light cancels all color responses in our visual system. White is considered achromatic or non-colored.

Summary

This chapter covered the basics of the nervous system. First, the basic anatomy of the neurvous system was describe indicating the basic distinctions in the anatomy between the central and peripheral nervous system and the basic divisions of the brain into forebrain, midbrain and hind brain. Next, the anatomy and function of the neuron was covered. The neuron is the most important functional neuron of the brain. Neuron has many important parts including the dendrites and somas that both receive input from other neurons (somas also have the genetic material of the cell), axons which send signals and terminals which communicate with the next neuron in the sequence. On actions, neurons communicate via action potentials. Action potentials are electrical signals carried by chemical means along the membrane of the axon. Action potentials follow the All-or-none Law; they are always the same size and do not shrink as they travel down the axon. Communication between neurons occurs at the synapse. Synaptic communication is a chemical process. The action potential's arrival at the terminal triggers a sequence of events that releases neurotransmitters into the synaptic cleft. The neurotransmitters bind to receptor molecules on the postsynaptic neurons an change the voltage in the postsynaptic neuron. Some synaptic connections are excitatory which make the postsynaptic neuron more likely to fire and others are inhibitory, which make the postsynaptic neuron less likely to fire. Summation of these postsynaptic potential at the axon hillock is what determines if a new action potential is likely to fire. To fire the summed postsynaptic potentials must reach the threshold voltage for that neuron.

Next the cortex was discussed. The cortex is the thin layer of cells that overlays the surface of most of the forebrain. Three organization principles of the cortex were discussed. First, the cortex is topographically organized. One can map a sensory experience onto the cortical surface. Second, the cortex is made up of six layers. For the purposes of this text, layer 4 is of particular interest as that is where sensory information will synapse. Third, geing from the surface of the brain through the layers of the cortex are columns. All cells in a column respond in some similar fashion, for example all might respond to pain. Finally, ways that neurons can help represent our experience of the world were discussed. This is sensory coding. Some coding can be done by a single neuron but more commonly many neurons are involved. The types of coding discussed were Law of Specific Nerve Energies, Frequency Coding, relative firing rate, and Opponent Processes.

Key Terms