

**Author's note to online readers:** The following two chapters may be shortened just a little.

There will be many illustrations, but I don't have permission to use most of them yet.

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## WAYS OF ADAPTING

Of all the millions of species of living things on Earth, creatures with brains are a tiny minority. In fact, creatures with nervous systems are a minority. Come to think of it, *creatures* of any sort are a minority; if by *creature* we mean an organism belonging to the animal kingdom. Bacteria, archea, protists, plants, and fungi—none of these things have a nervous system. Nervous systems can only be found in animals, and not even in all animals. By any measure—number of species, number of individuals, ecological impact, or sheer biomass—all those other groups outnumber us animals, which means that a nervous system is by no means a necessity for surviving in this world. Most living things do quite well without one.

But this doesn't mean that those other organisms they just sit there passively. Most living things are quite capable of responding to their environment, even without a nervous system. Many bacteria are able to move toward food and benign environments, and away from harmful environments. They are even quite speedy—bacteria with flagella may cover 100 body lengths per second; a feat no human can match. Protists are also responsive organisms. Amoeba pursue other microorganisms and engulf them. They also flee (in their slow, flowing way) from electric shocks or other insults. Plants keep track of the cycles of the days and seasons, dropping their leaves, growing new ones, and releasing pollen or seeds according to changes in day length and other cues. Some plants, like the Venus flytrap, feast on insects by grabbing them with appendages that look like tiny bear traps. But this is child's play compared with the tactics of the familiar corn plant. These can detect caterpillars munching on their leaves, and respond by releasing chemicals that attract wasps, who come and snatch the caterpillars. Even fungi are capable of behaving in surprising ways. Some, called Deuteromycetes, are predators. They snare passing roundworms or protists in tiny, noose-like loops, and digest them from the inside out.

Practically every living thing, then, is capable of simple behaviors and responses. Many of these are based on simple, physical mechanisms. Some flowers, for example, have spring-loaded stamens. When a bee lands, the stamens pop up and throw pollen on its back. Some responses are based on more sophisticated chemical messages. Sunlight falling on a plant causes a series of

chemical changes that results in more cell growth on the dark side of the plant, which causes the plant to bend toward the light. Some such simple responses in organisms without nervous systems cause changes in gene expression, while others simply run on a series of chemical changes, which are made possible, but not directly supervised by, the genes. Many behaviors, in organisms with or without nervous systems, rely on feedback. If a bacterium moves into an area in which it detects toxins, it stops, spins around, and goes off in another direction. This is negative feedback, which inhibits the action that leads to it. If a bacterium swims into an area rich in nutrients, positive feedback kicks in, telling it to keep on swimming.

These sorts of behaviors are a kind of adaptation—a change in form or function to meet the challenges of the environment. Some are short-term adaptations, as when a bacterium switches course for more hospitable environments, and some are long-term adaptation, as when a plant changes shape to absorb more sunlight. Either way, it is a different form of adaptation from Darwinian evolution by natural selection. Natural selection modifies the gene pool of a population of organisms over many generations. The kind of adaptation we are discussing here is much faster and more individualized, because it allows an single organism to adapt to its environment over time. It's a supplemental, and much faster form of adaptation.

Of course it is still tied to the genetic adaptation of evolution. For one thing, individual adaptiveness is a product of evolution. The *mechanism* of adaptation, such as the way plants grow toward light, is an evolved characteristic. So, while the particular adaptation—the shape of the individual plant—is not passed from generation to generation, the ability to change shape is. Second, as we have seen, genomes themselves are adaptive in the short term in the sense that different genes can be turned on or off as the need arises. What we have, then, is two linked forms of adaption working at once. The adaptation of populations works only across generations, which is why it has developed a supplement—the capacity for individual adaptation within a single life span.

## **SIMPLE NERVOUS SYSTEMS**

Individual adaption is an extremely useful trick, which is why it has evolved so many times, in so many different forms. While every organism is capable of it, the group that really mastered it was the animals. They did so over time, as needed. Sponges and other primitive animals are not especially responsive creatures. They don't need to be, because they don't go anywhere. The next branch of animals to evolve, those with radial symmetry and true tissues; such as jellyfish, corals, anemones, and hydras, were a bit more sophisticated. Not only were they more complex, but many of them were able to swim, at least during part of their life cycle. This increased mobility required a bit more savvy than the sponges possessed, and this was provided in the form of the first nervous systems. These simple systems resembled those of today's hydras and jellyfish (Figure .1), which have a diffuse network of nerves crisscrossing their body. There is no centralized brain, though some radial animals do have several clusters of nerves, called **ganglia**, that function as localized control centers.

Nervous systems became more centralized with the emergence of bilaterally symmetric animals such as flatworms. Flatworms, like radiate animals, are pottymouths. By this I mean they have only one digestive opening, which serves as both mouth and anus. Nonetheless, they are the simplest animals that can be credited with a true head, because one end tends to be in front when they move. Some flatworms, such as planaria, have simple light detectors called *eyespots* on this end, so they can vaguely see where they are going. They also have a cluster of nerves concentrated at the head end—the simplest system that can be called a brain. Flatworms have two nerve cords running down each side of their body, with smaller nerves projecting outward (Figure .2).

Most bilaterally symmetric animals, especially mobile ones, have their mouth, sensory organs, and brain all concentrated at the head. This makes sense, since the head is the first part of the body to make contact with new features of the environment (some of which need to be eaten, and some fled from). This concentration of organs around the head is called **cephalization**. Most bilateral animals are cephalized to some extent, although some, such as starfish and crinoids, have reverted back to radial symmetry. These creatures tend to have a diffuse, decentralized nervous system like that of a jellyfish or coral.

## WHAT NERVOUS SYSTEMS DO

### RUNNING THE SHIP: INTERNAL OVERSIGHT

Whatever their shape, nervous systems really have two main functions, both related to helping a complex organism function smoothly. The most obvious is to help the organism deal with its external environment. But an equally important function is to help orchestrate the complex internal processes needed to keep a multicellular animal functioning. It's easy to forget about this second function. We think of our brains as organs for thinking, but a large part of what brains—and nervous systems in general—do is help keep the body running smoothly; by monitoring levels of hormones, nutrient levels, body temperature, and so on. Of course, these functions were maintaining themselves long before nervous systems came along, through the interplay between the bottom-up self regulation of metabolic networks, and the more top-down control of the genome. What nervous systems do is add another level of top-down control, to supplement the other levels (Figure?).

The genome that is copied through every cell in the body is powerful, but its position is not optimal for taking a bird's eye view of the entire organism. This is why genes evolved that coded for the development of nervous systems; which are capable of monitoring things from an executive position, and making fast responses when the need arises. The genes have ceded some control to nervous systems in return for increased efficiency. It's a bit like the owner of a corporation hiring a president to help her run the business. The president—the nervous system—makes many of the moment to moment decisions, but in the long run, the owner—the genes—have the final say. If the nervous system does things that decrease the organism's reproductive fitness, that function will be selected against. While genes depend on nervous systems for help running the show, nervous systems depend on genes for their very existence. And for most animals, the two levels of control get along just fine, because the nervous system is basically set up to do what the genes "want" it to do. It is when nervous systems get sophisticated enough to get their own ideas that things get interesting, as we will see.

## **STEERING THE SHIP: COPING WITH THE OUTSIDE WORLD**

Besides internal housekeeping, the other function of a nervous system is helping the animal deal effectively with its external environment. This is especially important for mobile animals, which change their own environment by moving from place to place. A nervous system's response to the environment can be thought of as having three steps- *sensory input*, *internal processing*, and appropriate *physical output*. Let's say a fish is swimming along and encounters a change in its environment—another fish swimming its way. It detects the other fish with sensory organs—its eyes in this case. Information from the eyes passes to the fish's brain for processing. If the brain concludes that the approaching fish is small and edible, it sends down an order for an appropriate motor response; something like: *pursue smaller fish, if pursuit is successful, initiate eating sequence*. If the brain decides that the approaching fish is larger and threatening, it sends down an order for a different motor response: *FLEE!*

## **THE TIMESCALES OF ADAPTATION: IMMEDIATE RESPONSE, SHORT-TERM LEARNING, AND LONG-TERM LEARNING**

What the nervous system is doing is searching for patterns in its environment, and trying to respond to those patterns in an appropriate way. A key feature of nervous systems is that they are able to adapt to patterns at multiple timescales. The appearance of a fish requires an immediate adaptation, because it is a pattern appearing in the here and now. But such immediate patterns can add up to enduring patterns; regularities that the immediate patterns can be expected to fall into. The response of a fish to another fish is based on such an enduring pattern—smaller fish may be tasty, while larger fish may think you are tasty. One way to deal with such long term patterns is to have a hard-wired response, so that the nervous system always responds in the same way—big fish means flee, little fish means chase. This works best if the environment or the animal's lifestyle is extremely simple, and the patterns are very regular. But if the environment is unpredictable, or the animal has a complex lifestyle, then hard-wired responses may not work

well. These situations call for more flexibility. They call for the ability to learn.

Learning is a very sophisticated form of individual adaption, where an animals modifies not just its body, but its behavior; and not just on a moment-to-moment basis, but on a long-term, flexible basis. An animal that can learn has the ability to improve, with experience, its ability to respond to changes in its world. Learning and memory, then, are inseparable. Learning is the process by which memory is formed. Memory is the storage of what is learned. They are two ways of looking at a single process, the retention of information about persistent patterns in the world. Of course, I am speaking in very general terms here, because learning and memory can take many forms. Let's focus on learning here. Learning can be as simple as learning to ignore a repetitive stimulus, or as complicated as becoming fluent in Chinese. Also, some types of learning deal with more extended timescales than others. Learning can occur in the short term, as when we remember a phone number for a few minutes. It can also occur in the long term, as when we remember a name, or how to ride a bicycle after many years. So, the adaptation performed by the nervous system can be thought of as occurring in three basic timescales- immediate, short-term, and long-term. Each of these functions are based on different mechanisms. To understand these mechanisms, we need to look at the basic building blocks of the nervous system.

## **THE BASIC UNITS, AND HOW THEY WORK TOGETHER**

Nervous systems have two basic kinds of cells. There are **neurons**, which are the cells that transmit information in the form of nerve impulses. Neurons are far outnumbered, however, by so-called **glial cells**. Glial cells make up the neurons' support staff—they help with structural support, development, electrical conduction, and other such functions. Like many support staffs, glia are numerous, vital, and underappreciated. They are out-shined by the neurons, which are the stars of the show.

A neuron is a very specialized, elongated cell that carries impulses from one end to another (Figure). At one end are branches called **dendrites**, which usually, but not always, emerge from the **cell body**; the widest part of the cell which contains the nucleus. The dendritic

branches converge into a trunk called the **axon**. Drawing of neurons in books tend to give a distorted view of neurons, because the page isn't big enough to show the full length of most axons, which may extend for several centimeters. In humans, the neurons connecting the lower spine to the feet can be a meter long. In larger animals, they are no doubt even longer. At the end of the axon is another set of branches, with button-like tips called **axon terminals**.

A neuron is basically a cable with branches at each end. Nerve impulses travel from the dendrites, down the axon to the axon terminals, and then on to the dendrites of the next neuron. But there are two important points to make here. First, impulses don't just travel from one single neuron to another. Most neurons receive inputs from many other neurons (often thousands) and provide axonal inputs to many others. Second, neurons don't quite touch one another. Between each axon terminal and the next neuron is a tiny space called a **synapse**<sup>1</sup>. Nervous systems are a bit like Chinese music, where the spaces between notes are as important as the notes themselves. The synapse—the space between neurons—is just as important as the neurons for transmitting signals down nerves. Both neurons and synapses transmit impulses, and they do so in different, but complementary, ways.

## NEURONS AND THEIR POTENTIALS

Let's look at how neurons do it first. The impulses that travel down an axon are electrical. Like many cells, neurons have a different electrical charge inside their membrane than outside. *Unlike* most other cells, however, neurons are able to rapidly change their internal charge. A resting neuron is negatively charged on the inside compared to the outside, mostly because many of the proteins and other molecules inside have extra electrons. In other words, they are negatively charged *ions*. The difference in charge across the membrane is called a **potential**, because there is potential energy between the two charges. The potential of a resting

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<sup>1</sup>Remembering which direction an impulse goes in a nerve cell is one of those simple things that is hard to keep straight. The mnemonic device I use is "DAT'S right" (Dendrites, Axon, Terminals, Synapse).

neuron is called the **resting potential**. The negative resting potential is kept at a constant level by transport proteins which straddle the membrane. These escort positively-charged sodium ions (which tend to migrate inward) back out; and escorts positively-charged potassium ions (which tend to migrate outward) back in. This *sodium-potassium pump* acts something like a bouncer—it maintains a desirable atmosphere inside by letting some people in, and throwing others out.

When the neuron transmits an impulse, it does so by suddenly changing the concentrations of these positive sodium and potassium ions. It does this based on input from other neurons, which changes the resting potential, making the inside of the neuron more positive or more negative. If the cell interior becomes positive enough, it reaches a threshold which causes an **action potential**, where the inside of the neuron briefly becomes more positive than its surroundings. The action potential transmits itself down the axon to the axon terminals, thus carrying an impulse from one end of the neuron to the other. Here's how this works. When the threshold is reached, a membrane channel, or *gate*, opens. This lets in sodium ions, causing the inside of the neuron to suddenly become more positive than the outside. Next, the sodium gate closes and a potassium gate opens, releasing positively charged potassium and returning the cell to a negative charge. Since the potassium gate closes slowly, the cell actually becomes more negative than it was before the action potential. This keeps it from firing again for a brief period, called the *refractory period*. The action potential is an all-or-none affair, in the sense that the spike of positive charge has the same magnitude every time. But it is not all or none in the sense that it happens to the whole neuron at once. The timing of the potassium and sodium gates is such that the action potential begins at the dendrite end of the cell and propagates itself down the axon to the axon terminals.

## **SYNAPSES AND THEIR POTENTIALS**

When the action potential reaches the axon terminals, synaptic transmission gets underway. Vesicles inside the terminal bind to the cell membrane and release their contents into the synapse. These contents are called **neurotransmitters**, and their job is to change the resting

potential of the next neuron, by opening or closing ion channels. Most neurons release only one kind of neurotransmitter. Some cause the next neuron to become more negative, thus pushing it farther from its firing threshold. A synapse filled with such neurotransmitters is called an **inhibitory synapse**. Some neurotransmitters make the next neuron more positive; an **excitatory synapse**. If the next neuron reaches its threshold, it will fire; carrying the impulse one more step down the line. In effect, each neuron is making a decision whether or not to fire, by adding up the combined input of all of its synapses; both excitatory and inhibitory. If the excitatory ones win out, bringing the potential up to the threshold, the neuron will fire, carrying the impulse another step down the line.

Nerve impulses, then, get carried along through alternating media—electrical signals within neurons, and chemical signals between neurons. These two processes are different in important ways. For example, an axon potential is an all or none event. The internal charge of the neuron can only vary continuously until it reaches its threshold. Once that happens, the action potential is the same every time—same voltage, same duration. This means that neurons can't respond to a stronger stimulus by firing more powerfully. Instead, they fire more *frequently*. A weak stimulus results in just a few action potentials, while a strong stimulus results in a staccato barrage of them, limited by the refractory period between potentials.

This all-or-none transmission changes at the synapses, however. Across the synapse, the strength of transmission depends on how much neurotransmitter is released, and *that* depends on how many action potentials reach the synapse. Neurotransmitters, then, build up continuously in response to the discrete action potentials. So, the strength of synaptic transmission is coded by continuous changes in *amplitude*, not by discrete *frequency*. One might say that neural impulses are binary, while synaptic impulses are analog. The nervous system works by transmitting information in both ways, retaining the advantages of each.

## **PATTERNS OF CONNECTION: NEURAL PROCESSING**

Of course, the point of a nervous system is not to simply transmit information. The point

is to *process* information; turning a set of stimuli into a coherent perception, and then responding with an appropriate action. Impulses need to be transformed in their journey through the nervous system. The way synapses and action potentials work gives us clues as to how this process might work. A filtering process is at work at each neuron, when it “decides” whether and how often to fire based on all the excitatory and inhibitory inputs it receives from other neurons. Let’s be very, very simplistic and imagine that an animal has a neuron that, if it fires, causes the animal to flee the scene. Some animals, such as squid and crayfish, do in fact have such nerves, which stimulate a jet of water or a strong flip of the tail, propelling the creature out of harm’s way.

Now, whether or not that neuron fires depends on its inputs from preceding neurons. The excitatory neurons will be firing if they are picking up signals associated with danger. For example, if the cells from the eyes detect a sudden darkening of the environment, due to a large form overhead, the escape neuron will start getting excitatory signals. But what if other signals indicate that the large form is actually made of many smaller forms? It could be a school of very edible minnows, not a predator. This will cause inhibitory signals to the escape neuron (and excitatory signals to other “pursuit” neurons). Whether the animal flees or not depends on whether the excitatory or inhibitory signals win out. And that will depend on whether more predator-detecting signals or food-detecting signals are going off, which is a fairly good indicator of what that dark form is. So, even though the escape neuron holds no internal image of a predator, it functions as a predator detector, simply by adding up inputs from other cells. This is an enormous simplification, of course, because most processing involves many neurons at every level, firing in parallel as well as sequentially. But it does illustrate the basic way that neurons process information, as each one makes its decision about whether or not to fire.

A key fact about nervous systems is that how they process information depends on the specific way neurons are connected together. Some strong connections arise on a moment-to-moment-basis. In the example above, some neurons momentarily became more strongly connected than others (both excitatory and inhibitory connections). This happened because, by firing rapidly, they built up a great deal of neurotransmitter in the synapses connecting them to other neurons. However, some connections between neurons are stronger than others, *even*

*before* they start to fire in response to a stimulus. Neurons involved in detecting big teeth (to take a simplistic example) will be strongly connected to others associated with other features of predators, such as shark-like fins. These neurons will be predisposed to influence each other strongly, so that one does not have to fire strongly in order to cause the other to fire. (Of course, some neurons will be strongly connected in an inhibitory way, so that one is predisposed to cause the other *not* to fire.)

## TIMESCALES AGAIN

So, how strongly neurons influence each other depends on how strongly they fire, and how strongly they fire depends on two things—the nature of the stimulus, and the strength of the preexisting connections between them. This brings us back to the different time scales of adaptation. In the example above, an animal is adapting immediately to a current situation, a pattern in the environment right then. But once again, some patterns can be expected to repeat. Most predators have similar features, as do many kinds of prey. This is where it becomes handy to have a specific pattern of connections between neurons, not just as the need arises, but over longer periods. This way, the animal will be pre-adapted to respond to patterns that show up again and again.

One way of doing this is to be hard-wired from birth, with a pattern of connections tuned to cause a stereotypical response to common situations. Many animals are partly hard-wired this way. If a toad sees a small dot move past, it will always do the same thing—zap the dot into its mouth with its tongue, blink its eyes, and wipe its mouth with its front leg. Same thing every time. Now, this works fine if the environment is fairly predictable, and small, moving dots can be expected to be edible bugs. But cruel children sometimes exploit the toad's inflexibility by rolling ball bearings past. The poor toad will become quite full of these, blinking its eyes and wiping its mouth with apparent relish each time it eats one. Such unpredictability in the environment makes it useful to be a bit more flexible; to be able to change one's neural wiring as the need arises.

Such changes constitute learning—an adaptiveness not just in the immediate term, but over

longer terms. Learning always seems to involve a change in the connections between neurons. Let's look at two very basic kinds of learning--**habituation** and **sensitization**. In habituation, an animal is given a mild stimulus, such as a light touch, which causes it to jerk away in the opposite direction. If the animal is touched repeatedly, however, it responds less and less strongly, until eventually it hardly responds at all. It has gotten used to the stimulus—learning that it is not worth paying attention to. Sensitization, on the other hand, is a way of learning to pay very close attention to a stimulus. If an animal is given a sharp poke instead of a light touch, it will of course jerk away. But the sharp poke causes a very different reaction to the next stimulus. Instead of getting used to it, the animal will be hypersensitive to it; jerking away violently even from a light touch. Both habituation and sensitization make good biological sense. One should ignore an inconsequential stimulus, but one should try to avoid another painful one.

Even the simplest animals with nervous systems are capable of sensitization and habituation. Scientists have figured out the neural bases of both by studying a kind of mollusc called a sea snail, or *Aplysia*. Sea snails look like enormous land snails (they are around ten inches long) that swim along by waving winglike appendages called parapodia. On the creature's back, in between the parapodia, is a structure called a mantle. A gill sometimes extends from underneath the mantle. Sensitization and habituation are studied by touching the mantle, which causes the gill to withdraw. Sea snails have a series of paired ganglia (nerve bundles), each of which controls a different function. The gill-withdrawal reflex is controlled by a single pair of ganglia, which has allowed scientists to study the individual neurons involved in sensitization and habituation, giving them a direct glimpse at mechanisms by which neurons change their connection strengths.

Sensory neurons from the sea snail's mantle connect to motor neurons enervating the gills, sometimes directly, and sometimes via an intermediate neuron called an interneuron. Habituation is controlled by synapses directly connecting the sensory and motor neurons. The basic mechanism is fairly straightforward—the sensory neuron puts out less neurotransmitter every time it fires, so the motor neuron responds less and less strongly. Since the motor neuron's response becomes weaker, so does the gill withdrawal reflex. Of course, this is the simple version. The

detailed mechanisms of this effect are still being worked out, but it is still impressive to discover the basic way that one neuron diminishes its influence on another.

The mechanisms of sensitization, on the other hand, have been worked out in exquisite detail. The basic mechanism of sensitization is just the opposite of habituation—instead of releasing fewer neurotransmitters with repeated activation, a sensitized neuron releases more. This means the motor neurons causing the gill reflex will respond more strongly to the same degree of activation in the sensory neurons. The increased release of neurotransmitter by the sensory neuron seems to be mediated by an interneuron, which releases a neurotransmitter called serotonin. Serotonin causes the sensory neuron to keep its potassium channels closed longer than usual. Since the release of potassium is what returns the neuron to its resting potential, these closed channels have the effect of keeping the axon terminals positive for a longer time, which means they release more neurotransmitter.

If a response to a current situation is a form of immediate adaptation, learning is an adaptation acquired across many situations. Learning occurs over extended periods of time. How extended depends on the type of learning. Some types of learning are short term; they last for a few minutes, hours, or days. The mechanisms for sensitization and habituation that we discussed above are short term forms of learning. If you habituate a sea snail, and then leave it alone for a few hours, you will find that the habituation has disappeared. The same is true for sensitization. However, if you keep sensitizing or habituating the poor creature several times a day, and then stop, the response can remain for weeks. This is long-term learning, and it seems to rely on different mechanisms than short term learning. Long term sensitization is associated with an increase in the number of synapses between sensory and motor neurons, while long-term habituation is associated with a decrease in synapses. Relatively permanent changes in the synapses and neurons also seem to be involved, such as changes in sensitivity to neurotransmitters, and changes in gene activation.

We can pass over the detailed mechanisms by which neurons change their connection strengths. The key point is that those mechanisms differ between short-term and long-term learning. Short-term learning relies on temporary changes in the connection strength between

neurons, usually as a result of changes in neurotransmitter release. Long-term learning relies on more permanent, structural changes in neurons and the synapses between them. The types of learning we have discussed so far are very simple, but the distinction between long-term and short-term learning seems to hold for more sophisticated kinds as well. And now it is time to move on to those more sophisticated kinds of learning, as they occur in the complex nervous systems of vertebrates.

## THE VERTEBRATE NERVOUS SYSTEM

### A HIERARCHY OF NERVOUS SYSTEMS

The basic plan of the brain and nervous system is similar for all vertebrates. It is a highly centralized system, with a single nerve cord connected to a well-developed brain. The brain and spinal cord constitute the **central nervous system**. The **peripheral nervous system** includes all the nerves leaving the brain and spinal cord for the rest of the body. To get a better idea of this arrangement, it helps to look at a cross section of a vertebrate spinal cord, as in Figure .

The first thing one notices about this cross section is its two-tone color scheme. The middle section has a grayish hue, while the outer section and the nerves leaving the cord are white. The tissues making up these regions are called, descriptively enough, **gray matter** and **white matter**. Grey matter is grey because that is the color of the cell bodies of the neurons that make up the spinal cord. White matter is composed of the axons stretching from those cell bodies to other parts of the body. This white color, which is unique to vertebrates, is the color of a fatty substance called **myelin**, which is produced by glial cells called Schwann cells. These form sheaths of myelin that coat most of the axon, except for small spaces called *nodes of Ranvier*. Roughly speaking, this coating has the effect of insulated the axon, allowing impulses to travel much faster than in unmyelinated neurons. Vertebrate nervous systems can send signals across the body much more efficiently than those of invertebrates, which is one reason that vertebrates tend to be relatively large, complex creatures.

As the figure shows, the peripheral nerves branch in two before connecting with the spinal cord. Each branch contains different kinds of neurons. The dorsal branch contains sensory neurons, which carry impulses in from the rest of the body. The ventral branch contains motor neurons, which carry impulses back out to the body. These are the fundamental divisions within the peripheral nervous system—the **sensory division** and the **motor division**. The motor division, in turn, can be subdivided into the **somatic nervous system** and the **autonomic nervous system**. Figure summarizes the divisions of the nervous system.

For the most part, the somatic nervous system controls the body's movements, and tends to be under voluntary control. The autonomic nervous system is in charge of regulating internal organs and glands, and it is not under voluntary control. The autonomic system, can also be divided in two, into the **sympathetic** and **parasympathetic systems**. The parasympathetic nervous system usually prepares the body for resting activities—by slowing the heart rate and increasing circulation to the digestive system, for example. The sympathetic nervous system has the opposite function. It prepares the animal for emergencies; for fight or flight situations. It increases heart and breathing rates, and increases blood flow to skeletal muscles.

As Figure shows, the autonomic nervous system is based on a separate set of neurons from the somatic nervous system. Both share the nerve bundles leaving the spinal cord, but the autonomic neurons are routed through ganglia (bundles of nerves) outside the spinal cord, and on to the internal organs. The sympathetic system emerges from the middle spinal cord, moving through ganglia just outside the cord. The parasympathetic system also has external ganglia, but it emerges either directly from the lower brain, or from the lower spinal cord. The opposing functions of these two systems help the animal match its bodily functions with its current situation, whether that situation is relaxed (parasympathetic) or alarming (sympathetic).

## **THE VERTEBRATE BRAIN**

As we saw in the last chapter, all chordates have a hollow nerve cord. In vertebrates, the brain develops from three bulges in the front end of the nerve chord, which become the three main

divisions of all vertebrate brains—the **forebrain**, the **midbrain**, and the **hindbrain**. Figure shows the brain of a typical adult fish, which illustrates the basic pattern on which all vertebrate brains are built.

## THE FOREBRAIN

The forebrain of a fish is mostly concerned with processing smells, which is evident by the prominent **olfactory bulbs**. These bulbs connect with the **cerebral hemispheres** (I am using plurals because the brain is mostly bilaterally symmetric, so most structures are mirrored on each side). The cerebral hemispheres in fish process olfactory information, but they also play a role in integrating inputs from various parts of the brain. This role has been greatly expanded in more recently evolved vertebrates.

Inputs from other areas of the brain reach the cerebral hemispheres through the **thalamus** (not visible in Figure ), which acts as a sort of central relay station between various parts of the brain. The position of the **hypothalamus** can be remembered by its name, which means “below the thalamus”. The hypothalamus helps control the state of internal organs. It is densely connected with the autonomic nervous system, as well as the **pituitary gland**, which regulates internal organs and glands by secreting various hormones. Basically, the hypothalamus is involved in switching the body’s overall state in response to the external situation; states which are associated with emotions and urges, such as fear, pleasure, hunger, and anger. As it has been crudely put, the hypothalamus helps control the four F’s of animal behavior—feeding, fighting, fleeing, and sex.

## THE MIDBRAIN

The midbrain is mostly concerned with sensory processing. The **optic nerves** connect the eyes with a part of the brain called the **optic tectum**, which processes visual information. Inside the eyes, the optic nerves connect with the rods and cones of the retina. The retina develops from

cells that migrate from the brain during development, so it can really be considered a part of the brain. The optic nerves cross over each other on their way to the brain, so that input from the left eye is processed by the right lobe of the optic tectum, and vice versa.

## THE HINDBRAIN

The hindbrain is the part of the brain that connects with the upper spinal cord. It has three main parts: the **medulla**, the **pons**, and the **cerebellum**. The medulla looks like a slight bulge in the spinal cord as it makes the transition into the brain. The pons is a larger bulge on the anterior side, and the cerebellum is a protrusion on the dorsal side. The midbrain and pons function as pathways through which signals from the spinal cord must pass to reach other parts of the brain. Like the nerves from the eyes, nerves from the spinal cord also cross over to the opposite side of the body, so that the left side of the brain controls the right side of the body. (Why this happens is unknown, but one guess is that early vertebrates were able to bend away from harm by activating muscles on the opposite side of the body from the threatening stimulus.) The hindbrain also processes information from vibration and touch receptors. Terrestrial mammals with eardrums pick up vibrations in the air. We call those vibrations sounds. Fish and larval amphibians detect vibrations in the water with the lateral line systems extending down their sides. The pons and medulla also help with basic functions such as breathing, digestion, and arousal.

The cerebellum helps coordinate motor activity, harmonizing motor commands from the cerebrum with information from the sense organs about things like joint position and muscle contraction. Basically, the cerebellum promotes balance, smoothness, and precision of movements. Damage to the cerebellum tends to hurt balance or result in jerky, inaccurate movements. Fish have a rather large cerebellum because, unlike terrestrial animals, they need to navigate through three dimensions.

This is the basic structure of the brain for all vertebrates. Of course, this structure has been modified and tuned in various ways, among various groups. Creatures that rely more on smell, such as rats or sharks, have relatively large olfactory bulbs, while those that rely on sight

have larger optic tecta. Some changes have occurred with the rise of new groups of vertebrates. In birds and, especially, mammals, the basic vertebrate brain has become larger and more complex, giving its owners the capacity for flexible, sophisticated behaviors. Let's take a closer look at the sophisticated brains of our own group, the mammals.

## **THE MAMMALIAN BRAIN: A CLOSER LOOK**

Being vertebrates, mammals have the basic three-part division of the brain, but the forebrain is quite large. The two main parts of this enlarged forebrain are the limbic system and the cerebral cortex. The word "cortex" comes from the Greek for tree bark. This is apt, because the cortex is a thin sheet of grey matter, formed by the cell bodies of neurons. Each cerebral hemisphere, then, is really just a thin rind of grey matter (cell bodies), connected by white matter (axons) to structures below. In mammals with big brains, the cortex has to be folded to fit into the skull, producing convolutions. Convolutions that fold outward are known as **gyri** (singular **gyrus**) and those that fold inward are known as **sulci** (singular **sulcus**).

Now let's look at a single half of the brain, cut right between the two cerebral hemispheres. The structure called the corpus callosum, arcing up over the thalamus, is the main link between the two hemispheres, consisting of enormous numbers of axons. The first gyri of cortex around the thalamus and corpus callosum form the limbic lobe (limbic being Latin for "border"). These gyri are connected with subcortical structures around and between the corpus callosum and thalamus to form the **limbic system**. This system is devoted to emotional and appetitive processing, which especially involve the hypothalamus and the **amygdala**. Mammals have a much more developed limbic system than other vertebrates, and a correspondingly wider range of emotional behaviors. The limbic system is also essential to the formation of long term memories. The main player in this function is the **hippocampus**. Some people with damage to both hippocampi have entirely lost the ability to form new memories.

The "border" areas of cortex that give the limbic system its name are less complex than other areas. The rest of the cortex is a phylogenetically newer region called the neocortex, which

is unique to mammals. The neocortex is made of six distinct layers of neurons (which allow some rather sophisticated processing, as we will see). These layers form a concentric division, from the inner to the outer cortex. But the cortex is also divided into different regions across its breadth. As figure shows, the broadest divisions in the cortex are the so-called **lobes**, the **frontal**, **temporal**, **parietal**, and **occipital lobes**, which are named for the bones of the skull that cover them. (Interestingly, the temporal bone is so named because hair on that part of the head is the first to turn grey, a time related, or *temporal*, process).

The cerebral lobes are not just physically distinct. They are functionally distinct as well, because each one has a broadly different task. In fact, the lobes are simply the broadest division in the cortex, which is minutely divided into different areas with different functions. Figure , for example, shows the primary sensory areas of the cortex, the places where sensory information first arrives at the cortex from the sense organs, via the thalamus (except in the case of smell). The primary auditory area is along the top of the temporal lobe, close to the ears from which it gets data. The primary olfactory area is not far from the nose, along the bottom of the frontal lobes. The primary visual area, on the other hand, is far from the eyes—at the back of the head in the occipital lobe. Touch sensations come in at the primary somatosensory area, a strip along the front of the parietal lobe, along the central sulcus. Just across the sulcus is the motor projection area, the main cerebral control center for movements.

The somatosensory and motor areas are a good illustration of a central fact about the cortex—it is *topographically organized*. What this means is that the spatial arrangement of sensory neurons from the rest of the body is roughly mapped in the spatial arrangement of neurons in the cortex. Each area of the somatosensory area, for example, gets signals from a particular area of the body, and adjacent areas of the body, such as the elbows and wrist, are usually represented by adjacent areas of cortex. The visual cortex is also topographically organized. The spatial arrangement of neurons in the retina is mirrored in the spatial arrangement of the visual area. Of course, these cortical mirrors are a bit like funhouse mirrors, as Figure shows. Some areas of the body, such as the face and hands, are more sensitive than others, such as the back, so they get more cortical representation. Similarly, the center of the retina is more

sensitive than the periphery, so it gets more cortical representation.

The areas of the cortex between the primary sensory and motor areas are called *association areas*. As the name suggests, these areas are devoted to connecting different primary areas, so that they can work together. But don't get the idea that these are just passive transit zones. The association areas take information from the primary sensory areas and refine it further. Once again, different areas perform different functions. However, this doesn't mean that every particular act the brain performs is accomplished in only one area. Each area does tend to perform one highly specialized function, but most complex perceptions, thoughts, or actions involve many such specialized areas working together. To flesh this idea out, let's take a look at one of the better understood aspects of brain functioning—vision.

## **SEEING INTO THE BRAIN**

Consider this the next time you spot the glowing eyes of a cat in your headlights—you are looking directly at that cat's brain. During development, cells from the brain creep forward into the eye to form the retina, the reflective lining at the back of the eye, so the retina can be considered a part of the brain. This is not just a technicality. Vision depends on a great deal of neural processing, and that processing begins immediately, in the retina. Visual processing is better understood than most brain function, so focusing on it provides a way of seeing into the workings of brain, both literally and metaphorically.

### **EYE TO BRAIN: CROSSING WIRES**

First of all, let's look at the wiring between the retina and the rest of the brain. Just as touch sensations on the right side of the body are processed by the left side of the brain, objects in the right side of the visual field are processed by the left side of the brain (and vice versa). Figure shows how this works. Actually, images of the outside world undergo more than one twist on the

way into the brain. Images falling on each retina are inverted by the eye's lense. The image is upside down, and the right side of the each retina detects the left visual field. The optic nerves from each eye meet at a spot just in front of the thalamus called the **optic chiasm**. Nerves from the right side of both retinas (which detect the left visual field) go to the right side of the brain. Nerves from the left retinas go to the left side. Normally, both sides of the brain are aware of the entire visual field, because they are connected by the corpus callosum, and because the eyes tend to roam all over the visual field. From the optic chiasm, the optic nerves go to a place on the thalamus called the **lateral geniculate nucleus**, or LGN, and then on to the primary visual cortex in the occipital lobes at the back of the brain.

## **THE INTELLIGENT EYE**

That's the large scale wiring. Now let's zoom in a little, to see how images are processed along this pathway. As figure shows, the retina has three layers of cells. Moving toward the back of the eye, the first cells we encounter are neurons called **ganglion cells**. These cells converge to form the optic nerve, which leads from the retina to the rest of the brain. The next layer, descriptively called the middle layer, contains several kinds of neurons which mediate connections between the ganglion cells and the final layer, the rods and cones, at the back of the eye. These are the receptor cells of the retina; the cells that actually detect incoming light. If it seems a little backwards that the rods and cones are at the back of the retina, so that light has to pass through a tangle of other cells to get to them, that's because it is. It would work much better if the rods and cones were in front, but the chance mutations that drive evolution never hit on that arrangement. Ironically, the eye is often cited by creationists as being "too perfect" to have been put together by evolution. The eye is amazing, but it is imperfect in exactly the way that products of evolution often are.

Rods and cones have different functions. Rods are insensitive to color, and overwhelmed by bright light, so they are mostly useful for night vision. We see daytime scenes mainly with our cones, which are sensitive to color. Cones come in three different types, which are (roughly

speaking) sensitive to blue, red, and green. The colors we see are the result of different relative activations of each kind of cell.

But color vision is complicated, far too complicated for this book. Let's pretend that the retina is only processing black and white images, so we can focus on how it detects changes in illumination, which is the basis for detecting shapes. This processing is centered around the ganglion cells. As we have seen earlier, the way a neuron processes information depends on its connections to preceding neurons or sensory receptors. Each ganglion cell is connected to several rods or cones, by way of other neurons in the middle layer. So, each ganglion cell is sensitive to light falling on the region of the retina occupied by the receptors connected to it. This region is called its **receptive field**. Now, if you shine light on the retina and record how different ganglion cells respond, you will find three different responses. Some fire when the light goes on, others fire when it goes off, and others fire continually as long as a spot of light is moving around in their receptive field.

This means that fairly sophisticated processing of the timing and motion of light is already underway by the time visual information leaves the retina. Since motion, like color, is also complicated, let's focus on the cells that register when light goes on or off. These come in two basic types, called **on-center** and **off-center** cells. On-center cells respond when illumination across their receptive field increases, while off-center cells respond when illumination decreases. But they send much more information to the brain than simple changes in the lighting. In fact, overall changes in lighting are not that important. If you open the shades on to a dark room on a sunny day, you may increase the overall illumination thousands of times. But you need to see the objects in the room as the same objects, regardless of how brightly they are lit. This is a difficult computational task, but it is one at which the ganglion cells excel.

To see how, we need to take a closer look at their receptive fields. On-center cells, like most neurons, are usually firing a few times each second. This rate of firing increases somewhat when a light is turned on that covers their receptive fields, which is how they detect increased illumination. However, their receptive fields are divided into two very different regions. If a bar of light is turned on that falls directly across the center of the receptive field, as in Figure, the cell

reacts wildly until the light goes off. However, if the bar of light misses the center, and falls across the periphery, the cell will not fire at all while the light is on. This is why they are called on-center cells, or sometimes, on-center, off-surround cells. As usual, this special capacity of the cell is based on its connections with preceding cells—it receives inhibitory impulses from cells in the periphery of its receptive field, and excitatory impulses from those in the center. The off-center cells are just the opposite of the on-center cells. Their basic firing rate is inhibited while a light shines across their receptive field, but is mildly excited when that light turns off. They react wildly when a bar of light is shone across their periphery, but not at all while it is shone across their center.

The point of the different reactions to light falling on different parts of the receptive field is that these ganglion cells are not just sensitive to changes in illumination over time, but to changes in illumination at different places on the retina. They are exquisitely sensitive to *edges*, places where light changes suddenly from one brightness to another (or from one color to another). Imagine that you are looking at a building from one corner, so that you can see two sides. Both sides are the same color, but one is catching more sunlight, so it is illuminated more brightly. Where the image of the corner—the edge between the two sides—falls on the retina, it affects different cells in very different ways. On the dark side, the off-center cells respond more and the on-center cells respond less, while on the light side the situation is reversed.

What this means is that the contrast between the two sides is enhanced. And contrast is what the retina is mostly concerned with—relative, not absolute, differences in brightness. A vivid illustration of this effect is an optical illusion called Mach bands. In Figure it looks as though each block gets darker from right to left. But this is an illusion. Each block is the same tone all the way across. The apparent difference is a result of contrast enhancement of the edges of the blocks, which exaggerates the difference in tone between each adjacent block. If you put your finger across one of the borders, the blocks on either side will look much more similar, because there is no longer a sharp edge to activate the contrast enhancement.

## **THE VISUAL CORTEX**

## THE FIRST STOP: THE PRIMARY VISUAL AREA

Keeping these processes in mind, let's look at what happens further down the visual assembly line. Ganglion cells connect to cells in the thalamus, which basically respond to the same things as the ganglion cells. Axons from these cells leave the thalamus for the occipital lobes, where they terminate at the fourth layer of the cortex (from the surface). From there, they link with other neurons leading to other layers of cortex, and to other parts of the cortex. But the visual cortex isn't just divided longways, into layers. It is also divided into columns, which run from the bottom to the top layer. These columns are the site of further processing of data from the ganglion cells. They contain neurons, called **simple cells**, that combine the input from ganglion cells, the way ganglion cells combine input from other neurons and receptors. Suppose, as Figure shows, that a simple cell has a receptive field that combines several on-center cells. If a bar of light is shone on the retina, this cell will only respond if the bar falls directly across the centers of the receptive fields of each ganglion cell. If the light falls to the side, across the peripheries of the cells, the simple cell will cease firing while the light is on. A diffuse light, or a bar of light with a different orientation than the line of centers, will cause no change in the rate of firing. This is where the columns in the cortex come in. Each column contains simple cells that respond only to edges with a particular orientation. Moving across the cortex, each column responds best to a slightly different orientation, through the full 360° of possible orientations.

## SPOT CELLS, LINE CELLS, AND.....GRANDMOTHER CELLS?

That is a very simplified description of what happens in the primary visual area. But it gives an idea of some basic principles of perception. First, processing is hierarchical, in that downstream neurons combine the input of many upstream neurons. Many cells combine to form the receptive field of ganglion cells, which in turn combine to form the input of the simple cells. So, the further upstream we go, the more selective the neurons tend to be, and the larger their receptive fields, because they are combining the input from more and more neurons. And, as the

name “simple cell” suggests, the process doesn’t end there. Other areas of the occipital lobes, beyond the primary visual area, contain even more specialized cells. Some, called **complex cells**, respond to edges with particular orientations, but only when those edges are moving in a certain direction. They may fire if the edge is moving down and to the right, but not if it is moving up and to the left. Other cells can be even more selective. One group of researchers tried for hours to get a neuron to fire by presenting all sorts of lines and bars moving in various ways. It finally fired, unexpectedly, when one of the researchers waved his hand. It turned out that it was specifically tuned to responding to objects with the shape of a hand. Other cells seem respond only to faces.

So how far does this process go? Are there, as it is commonly put, “grandmother cells”, which only fire when they see your grandmother? Is that how we perceive things, by assigning a single “end of the line” neuron to respond to every complex object out there? Probably not. There are several reasons this wouldn’t work. For one thing, if your grandmother neuron died, as neurons are doing by the thousands every day, you would no longer be able to recognize granny. Plus, such a scheme would be inefficient. We would need separate neurons for everyone we know or recognize. Most likely, we would also need separate cells to recognize them from different angles. It is almost certain that the hierarchical coding by neurons breaks down before it converges on single “grandmother” type neurons. So what does happen? We will return to this question later.

## WHAT AND WHERE: OTHER VISUAL AREAS

First, we need to look at what happens to visual signals after they leave the primary visual area, which is really just the first stop in cortical processing. Beyond the primary visual area are many other, more specialized, areas of visual processing. There are separate areas specialized for processing motion, form, spatial orientation, depth, face recognition, color, and many more. These diverse functions can be grouped into two main pathways, often called the *what* and *where* pathways (Figure). The areas of cortex between the occipital and temporal lobes are mostly

devoted to recognizing the objects being perceived, which is why this is called the “what” pathway. The location of the what pathway makes sense, because parts of the temporal lobe are concerned with explicit memory. Memory areas in the temporal lobe help the visual areas recognize what they are seeing, by comparing items in memory with those currently being perceived. The “where” pathway, on the other hand, moves from the occipital lobe toward the parietal lobe. As the name suggests, cortical areas in this region are concerned with making sense of the spatial arrangements of objects being perceived, and how they relate to the perceiver’s position. This also makes good sense, because the primary somatosensory area is right there at the front edge of the parietal lobe, where it can provide information from the body, to compare with information from the eyes.