3 The Minimal Brain: Building Simple Defenses and Seeking Rewards

With a system as complex as the brain, where should we start describing it? In this chapter, we describe the idea of a hypothetical "minimal brain" that allows an animal to defend itself and seek rewards, essential components of survival. How do sensations lead to actions through simple sensorimotor circuits? We'll see that action flexibility necessitates uncoupling sensory and motor components. In fact, a brain can be thought of as an entire circuit "in between" sensory and motor cells. This "solution" frees animals from acting simply based on sensory stimulation. Instead, a multitude of factors that encompass emotional and motivational variables are integrated with perception and action to allow successful navigation of the environment.

You are reading this book now, either on paper or on a high-resolution screen, by engaging an incredibly complex visual system. An imaging device, perhaps a new-generation magnetic resonance imaging (MRI) machine, trained on your brain would reveal a large array of visual areas, among many others, that participate in a fine orchestration that takes years to master (think back to elementary school). Now, look around you. Primates, including us, are used to this IMAX, spectacular worldview of detail and color. In primates, when researchers poll the various pieces, the "visual cortex" adds up to roughly a third of the entire cortex.

In the 1880s, experiments with both dogs and monkeys pointed to the occipital cortex as an important territory for vision. In the subsequent decades, the systematic study of clinical cases of patients with blindness, either complete or of one side of the visual field, led to the localization of the visual cortex in the occipital cortex in humans, too. A hundred years after Hermann Munk described his findings about vision in dogs and monkeys, David Hubel and Torsten Wiesel would be awarded the Nobel Prize for Medicine and Physiology in 1981 for their work on the visual properties of neurons in parts of the thalamus and several cortical areas. The centerpiece of their work was the description of how cells in the primary visual cortex (V1) generate their responses, allowing the visual system to respond to contours and boundaries—the basic building blocks of perceiving the shape of objects.

Humans who have lesions in this part of the brain are blind, with the extent of the blindness depending on how much cortex is compromised. Puzzlingly, this is not what George Riddoch, a temporary medical officer in the British army, observed when he examined wounded World War I combatants. Riddoch reported his findings in an article published in 1917, where he described how soldiers who had been blinded by gunshot wounds that had destroyed the visual cortex around the calcarine fissure could still see motion in their "blind" fields, though not much else (see Riddoch 1917).[1] (A fissure, also called "sulcus," is a groove in the cortex; a protrusion in the cortex is called a "gyrus.")

The findings reported by Riddoch and a few others lay dormant for many decades, most likely because they countered the prevailing view that occipital cortex was *necessary* for vision. In 1973, another study reported on the effects of gunshot wounds to the occipital cortex in the back of the head. This time other scientists paid more attention. The patients investigated admitted to no visual experience in the part of the visual field affected by the lesions—to them, they were blind there. Yet, they could move their eyes toward small visual targets presented in the "blind" parts of space if prodded enough by experimentalists. Admittedly, performance was poor, but statistical analysis suggested that it was better than random guessing. How could the patients accomplish this if they did not see the targets?[2] If it crossed your mind that the patients had gained some form of extrasensory perception following their tragic incidents, this is not what was going on. It turns out that there was a second visual system lurking underneath the cortex all along.

Two Small Hills on the Roof

We now know that residual vision is present in persons with a lesion to the primary visual cortex. They may detect the abrupt appearance of objects, movement, and several other visual properties. Indeed, an entire cottage industry of researchers has vigorously studied vestigial visual functions and their implications for understanding the brain, as well as visual consciousness—given that persons with remaining vision frequently are unaware of "seeing." The reasons behind patients' abilities are yet to be completely worked out, but much depends on two small hills in the midbrain at the top of the brainstem. The two structures, one on each side, are called the superior colliculus (where "colliculus" is small hill in Latin).[3] (The superior colliculus is very close to the area called PAG in figure 2.2.)

The retina senses light by transforming energy from photons into electrical signals that leave the eye through a bundle of cables. As discussed in chapter 2, these cables are made of axons, which convey electrical signals between neurons. Action potentials exiting the eye reach the visual cortex in the back of the brain by way of the thalamus. Interestingly, fibers from the retina project to several other places, too, with one group transmitting signals to the superior colliculus at the roof of the midbrain. It is visual processing in this area that is partly responsible for the lingering visual capabilities detected in humans with lesions of the primary visual cortex.

But humans pale in comparison to the skills displayed by tree shrews (they look like small squirrels with pointy noses). Even with the complete elimination of the primary visual cortex, tree shrews exhibit impressive visual behaviors; they avoid obstacles in their path and catch moving pieces of food.[4] Although tree shrews, like all mammals, have visual areas that are cortical, it appears that the balance of contributions to their visual abilities is altered. Humans without a primary visual cortex are blind (but, as noted, some of them demonstrate visual capabilities on careful testing); tree shrews fare much better, in no small part because of the participation of the superior colliculus in their visual behaviors.

Previously, we discussed how the cortex is comprised of layered sheets of neurons and the subcortex is poorly structured. In biology, "rules" always have exceptions, and though part of the brainstem, the superior colliculus is beautifully layered. The number of cell layers varies considerably across species, with some species, such as lizards, having as many as 14 layers (humans and other primates have seven or so layers). Across vertebrates, the top layers, which are the one receiving fibers from the retina, are "visual" and respond to stimuli with short-latency responses. (In vertebrates that are not mammals, the superior colliculus is called the "optic tectum" because it is clearly visible at the "roof" [in Latin, "tectum"] of the midbrain, as shown in figure 9.3. Throughout the book, I'll use "optic tectum" when more clearly referring to nonmammal species.) Retinal projections to the superior colliculus are topographic, meaning that the spatial layout of light hitting the eye (left/right, up/down) and triggering retinal responses is preserved in the colliculus. Cells in the colliculus thus form a *map* of the external visual space, allowing the colliculus to "know" where objects are in the world.

Across vertebrates, the superior colliculus contains intermediate and deep layers, too. The deep layers, in particular, drive action—for instance, head movements in toads and eye movements in primates. To produce movements, signals from the colliculus reach regions in the spinal cord, which themselves control head and eye muscles. Combined, circuits involving the top and bottom layers allow visual inputs to help direct body, head, or eye movements to salient events in the world (figure 3.1).

In all, the superior colliculus, by receiving visual signals from the retina and by driving muscles, accomplishes the essential sensorimotor transformation—whereby sensory stimuli trigger motor responses—required to interface with the world. Input-output arrangements, pretty much necessary for survival, are implemented by the nervous systems of the simplest organisms and, remarkably, can be accomplished by even a single sensorimotor cell (figure 3.2). In this case, the cell, whose body is embedded in the organism, has a *receptor* end that is sensitive to the external environment and an *effector* end that can cause movement of some sort (as simple as some form of contraction). But the single-celled solution is rather inflexible, of course: Pretty much every time the receptor senses something, the effector does its job. The solution, though costly, is to grow more cells in the "middle." And that is what nature did when given a few hundred million years. Indeed, all vertebrates have a superior colliculus—or more generally, a brain. Phrased differently, we can think of the brain, with all its different parts, as evolution's solution to the problem of uncoupling inputs from outputs (figure 3.3). Without this flexibility, animals are bound to perish.

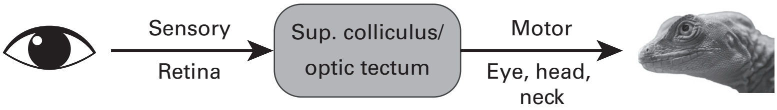

Figure 3.1
The superior colliculus (called the optic tectum in vertebrates other than mammals) receives visual signals from the retina and projects to structures that control movements. The region is often described as a fairly direct sensorimotor interface.

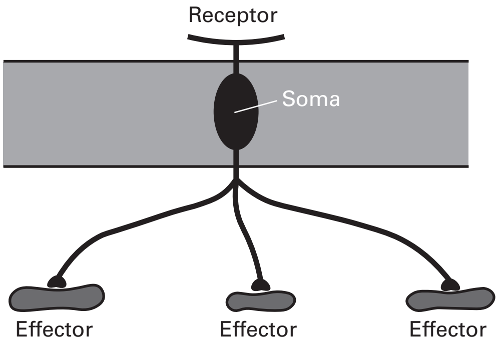

Figure 3.2
Sensorimotor neuron. The middle, elliptical part is the cell body (the soma). The receptor part is above and is sensitive to external stimuli. Effectors can be activated by the axonal ends of the neuron and are capable of generating some kind of tissue motion.

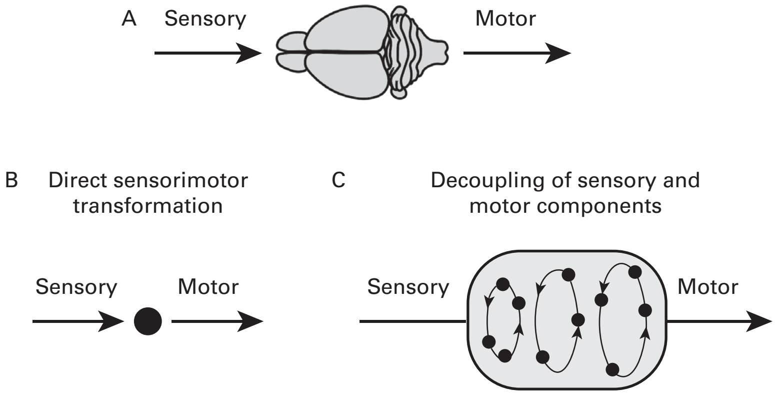

Figure 3.3
Input-output decoupling. (a) The brain solves the problem of decoupling sensory inputs from immediate actions. (b) A fairly direct sensory-motor transformation supports limited and rigid behaviors. (c) Uncoupling input from output provides increased flexibility. The ellipses indicate progressively larger circuits.

Decisions, Decisions

At all times, animals face a crucial three-way decision: Stay the course, move away, or move toward. In rodents, the superior colliculus participates in freezing in place, moving away, and defense-like behaviors.[5] Stimulation of the colliculus can produce a general arousal pattern (which includes large increases in blood pressure and heart rate) and analgesia (that is, processes that ameliorate pain), changes produced during naturally occurring defensive responses.

How is a stimulus classified as harmless, which may or may not be worth investigating further, as opposed to constituting an emergency that requires immediate action? The stimulus's position in the visual field plays an important role here. In small rodents, unexpected movement overhead (much like that of a predator) more likely triggers flight, whereas movement in the lower field (possibly a prey) more commonly elicits approach (figure 3.4). Thus, the superior colliculus could implement a rule much like this: If movement is overhead, flee; otherwise, if movement is in the lower field, consider further exploration. However, simple rules based on

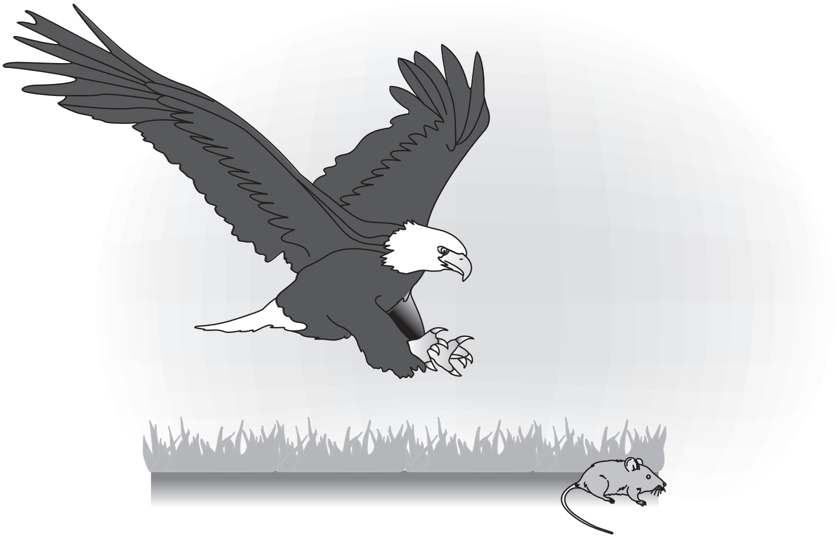

Figure 3.4
Many vertebrates react to stimuli in the upper visual field by fleeing. Stimuli in other parts of the visual field yield other behaviors, including exploration.

elementary stimulus features do not capture the flexibility of rodent behavior (think how hard it is to catch a rat!). For one, rats freeze more frequently to novel stimuli in unfamiliar environments, like an open field. (Freezing is the name given by researchers to a behavior characterized by the absence of overt activity.) Clearly, the context in which a stimulus occurs is paramount. Does the superior colliculus receive additional information that allows it to contribute to behavior in a more malleable manner?

Take the brain of the simplest groups of presently living vertebrates: lampreys, which are water inhabitants with elongated, eel-like bodies, and hagfish, sometimes referred to as slime eels. These animals are important to study because they provide clues about characters that were present in the common ancestor to all vertebrates.

The optic tectum of the lamprey contains five stacks of neurons. As in other vertebrates, the superficial layers receive optic fibers, and the deep layers send outputs that contribute to movements. What types of information do the intermediate layers receive? These layers receive inputs from several sensory sources, including the *lateral line*, a system used by some groups of aquatic vertebrates (including fishes) to detect movement and vibration in the surrounding water. The lateral line plays an important role in maintaining the orientation of the body and in schooling behavior and predation. Notably, in hagfish, the optic tectum receives projections from the hypothalamus which, as discussed below, participates in a wealth of bodily functions (including food intake, thirst, and sexual behaviors).[6] This is really a game changer, as it allows the superior colliculus not only to listen to multiple cues from the external world but also to receive signals from the *internal state* of the body—for example, Are nutrient levels low? Is it time for procreation?—and this is true across all vertebrates, including humans. In this way, the optic tectum's outputs have the potential to reflect multiple variables simultaneously, allowing context sensitivity to emerge as a natural consequence of its wiring and processing (figure 3.5).

The combined information can be used to consider how to react: Stay, approach, or withdraw? As stated, rats freeze in response to novel stimuli in unfamiliar environments more so than in familiar places. Though intuitive, this observation reflects a fundamental principle of brain function—*context sensitivity*. The brain does not simply react to sensory stimuli; instead, incoming data are incorporated into ongoing processing that encompasses the states of the brain and the body, explaining why the exact same stimulus

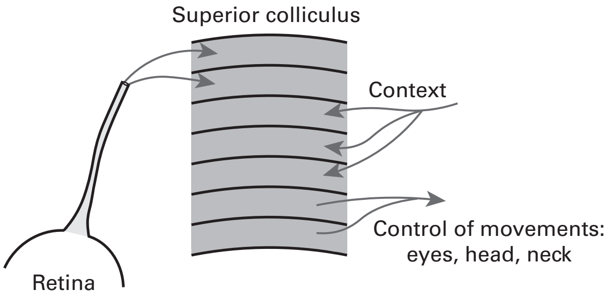

Figure 3.5
Inputs and outputs of the superior colliculus (layers shown schematically). In particular, context signals—for example, from the hypothalamus—allow the region to generate responses that depend on the animal's internal state.

exerts very different effects depending on the situation: in one setting a stimulus may lead to inquisitive approach, in another to moving away.

While the general problem of distinguishing an emergency signal from a neutral one is common to all animals, the details of what counts as an emergency vary markedly between species.[7] This is because adaptive decisions must take into account the relative costs and benefits of orienting toward something ("this is interesting") and escaping ("need to get out of here"). A major benefit of orienting is potentially acquiring better information (the eyes may now be directed at the object of interest); a major cost is loss of time. It's this kind of calculus that varies so much between species. An animal subject to intense predation might have laterally placed eyes that are excellent for panoramic vision but not for seeing details more centrally. In such a case, the gain of an orienting movement to bring a stimulus onto central vision could be relatively slight, whereas the costs of missing a predator would be high. In such animals, therefore, the balance should be tipped in favor of defensive responding, and this expectation is borne out by our experience with rats, rabbits, squirrels, and deer, for instance.

Shoring Up Defenses

The brain is bathed in a colorless fluid also found in the spine called the cerebrospinal fluid that, among other things, provides buoyancy and protection to the brain. The periaqueductal gray, or PAG (pronounced "pee-eyh,-gee"), is an area immediately adjacent to the superior colliculus and that surrounds a channel containing cerebrospinal fluid, hence the name (see figure 2.2). (Although I avoid abbreviations throughout the book, the name periaqueductal gray, also called central gray, is too unwieldy.) The PAG is where outputs from the superior colliculus (and many other brain regions) can be processed into more full-blown defensive programs. In several ways, the PAG can be viewed as an extension of the deep layers of the superior colliculus (Holstege 1991; Brandão et al. 1999).

Unlike the cortex and the superior colliculus, the PAG doesn't have layers. However, the region is not an amorphous bag of cells and seems to be organized based on columns aligned in parallel to the long axis of the brainstem (see figure 2.2). At least two columns of cells help organize defensive behaviors (Bandler and Shipley 1994).[8] In a rat or a cat, excitation of neurons in the "active" column generates behaviors such as facing and backing away or a full-blown flight reaction, and these are very similar to natural actions seen when the animal is threatened or attacked. Excitation of neurons in the "passive" column generates an entirely different response—namely, the cessation of ongoing activity and profound hyporeactivity, with the animal neither orienting nor responding to its environment. This type of freezing behavior is rather similar to that of an animal that has incurred an injury or after defeat in a social encounter (say, being chased by a larger animal). Notably, the PAG generates coordinated actions—that is to say, not simply isolated reactions (like a knee-jerk reflex) but full-blown behaviors. Thus, when engaged by the superior colliculus, the PAG can assist in the production of defensive actions that are beneficial at that point in time.

Seeking Out Rewards

Survival is as much about getting out of the way of danger as it is about keeping the body (think food) and species (think sex) going. When should an animal approach something? Interestingly, the PAG is not all about defense but participates in *appetitive* behaviors, too—that is, those behaviors that increase the likelihood of satisfying specific needs. Sex, for one, is tricky business. Not only are some species hierarchical, with the alpha of the pack having mating privileges, but in many cases females are only receptive during specific periods. Navigate this system poorly and you could end up badly injured.

Lordosis behavior, also called "presenting," is a body posture adopted by many mammals, including rodents, felines, and elephants, that indicates female receptivity to copulation. The body position during lordosis is often crucial to reproduction, as it elevates the hips, thereby facilitating penetration by the penis. Lordosis is commonly seen in female mammals during estrus. Interestingly, the PAG contributes to lordosis behavior, as suggested by impairments in this type of behavior when the structure is lesioned.

The midbrain, where the superior colliculus and the PAG are located, contains other structures that are quite important for appetitive behaviors. A region called the substantia nigra (so named because it appears darker than neighboring areas in chemical preparations) has received a great deal of attention. The superior colliculus has direct connections to the substantia nigra and, importantly, can cause rapid visual activation of neurons there.[9]

The reason the pathway from the superior colliculus to the substantia nigra is particularly noteworthy is that the latter synthesizes and uses the neurotransmitter dopamine. Dopamine, by its turn, plays a significant role in the functions of the striatum, where dopaminergic processing (that is, cellular mechanisms that use dopamine as a key neurotransmitter for neuronal signaling and communication) is important during the processing of novel or salient stimuli. Dopamine has received enormous attention because of its involvement during *reward* processing, including approaching objects previously associated with liked foods. Thus, the pathway from the superior colliculus to the substantia nigra allows the former to participate in appetitive actions rather directly. This is especially the case given extensive connections from the substantia nigra to the striatum and the latter's participation in *motivated behaviors* (for example, "though it might be effortful, I'll move along this path if it brings me closer to obtaining what I want").

Neurotransmitters: A Short Detour

Neurons communicate with one another through chemicals released at their synaptic contacts. Several classes of neurotransmitters have been uncovered, each of which leads to a maze of neurochemical complexity. A peculiarity of several neurotransmitters is that they are synthesized in only a handful of areas. Yet they punch way above their weight because the areas that produce them reach large swaths of the brain through their extensive anatomical connections—what we call "projections systems." The clearest example is norepinephrine, which is contained in only a few small collections of cell bodies in the brainstem. Remarkably, anatomical pathways from these sites go almost everywhere, including cortically and subcortically, enabling this molecule to influence cellular signaling throughout the brain.

Dopamine, too, is manufactured in only a few areas, one of which is the substantia nigra. The dopamine-containing cells there project to the basal ganglia, and this system (substantia nigra plus basal ganglia) has been extensively studied because it is at the root of Parkinson's disease. In the people affected, dopaminergic neurons in the substantia nigra die, causing the symptoms of the disease: most notably, tremors and repetitive movements and difficulty in standing and initiating movements such as walking. Fortunately, the motor impairments can be greatly ameliorated with the administration of L-DOPA, a chemical precursor to dopamine that increases its concentration in the brain.

In the early 1980s, the idea that dopamine is important for motivation and is linked to reward and reinforcement took shape, and since then a tremendous volume of work has shown ways in which this molecule is involved in these processes. How dopamine-related mechanisms are altered in addiction is a question that is actively researched. Most drugs that lead to addiction, including psychostimulants like amphetamine, increase levels of dopamine in the striatum, which can be verified by using an imaging method called positron-emission tomography (PET) that uses small amounts of radioactive drugs to detect specific chemicals in the brain. Studies using this technique show that the participants who display the greatest increase of dopamine after taking drugs are also the ones reporting the most intense “high” or feeling of euphoria (Volkow et al. 2009).

It is not too surprising, therefore, that dopamine is at times treated almost like a “reward molecule.” This infelicitous interpretation is common in the general media and in nonspecialty books. Unfortunately, it is also how some neuroscientists speak. But there is no such a thing as a “reward molecule”—the message is not in the molecule.[10] A particular neurotransmitter is involved in multiple functions, and its effect will vary based on the brain region (and circuit) where it operates, including the behavioral context in question. For one, dopamine in the striatum is not exclusively related to motivationally positive events; the processing of negative stimuli involves this molecule, too. Thus, dopamine is not a “reward molecule” for the same reasons we wouldn't call it a “movement molecule” (given the motoric impairments seen in Parkinson's patients).

This tendency to associate one neurotransmitter with one function is a conceptual shortcoming that impedes progress. Consider the involvement of dopamine in the devastating mental disorder of schizophrenia. In 1949, a French surgeon observed that a chemical created as a new type of color dye in the nineteenth century had a markedly calming effect on some surgical patients (just exactly how they decided to administer chemical dyes to patients is itself quite perplexing).[11] Soon afterward, a related dye was found to have beneficial effects on schizophrenics, and in 1954 it was approved in the United States as a treatment for this condition. The chemical, called chlorpromazine, doesn’t cure schizophrenia but can attenuate the most severe so-called positive symptoms, such as false-beliefs (like the thought that one’s behaviors are being closely monitored and recorded) and disordered thought.

The success of chlorpromazine and other more effective drugs (like haloperidol) led researchers to the “dopamine theory” of schizophrenia (Crow 1980): Drugs that have therapeutic effectiveness (they have antipsychotic effects) *antagonize* dopamine action. According to this framework, dopaminergic projections from the midbrain to the cortex and subcortical structures is overactivated in schizophrenia, dumping too much of this neurotransmitter in the recipient territories. Although current understanding of the role of dopamine in this mental disorder is considerably more nuanced, we can draw the following point from the basic dopamine theory: schizophrenia is not “caused” by dopamine but by the dysregulation of multiple circuits containing dopamine (and many other molecules) in rather complex ways.

Internal Context Signals: Am I Injured?

Processing by the superior colliculus benefits from signals that convey the organism’s current state. Chief among the structures that provide this information is the hypothalamus. As the name implies, the hypothalamus is located just below the thalamus (neuroanatomists weren’t very imaginative here); it’s also just above the brainstem. By the first years of the 1900s, the hypothalamus was identified as an anatomical entity surrounding the third ventricle (ventricles are cavities in the brain that are filled with cerebrospinal fluid). In 1904, Ramon y Cajal (encountered in chapter 2) described several “nuclear formations” (masses of neurons) forming the hypothalamus.

In 1929, Harvey Cushing, considered by many to be the father of modern neurosurgery, described the functions of the hypothalamus in this way: "Here in this well concealed spot, almost to be covered with a thumb nail, lies the very mainspring of primitive existence—vegetative, emotional, reproductive" (as cited by Card, Swanson, and Moore 2003, 795).

Since the 1920s and 1930s, our knowledge of hypothalamic function has greatly expanded. Current understanding concurs with the earlier notion that the area is involved in multiple "basic" life-preserving operations, including complex homeostatic mechanisms, in addition to contributing to neuroendocrine outputs (the endocrine system involves a network of glands that produce and release hormones that regulate many body functions). As we'll cover in chapter 5, the hypothalamus participates in a bewildering array of processes having to do with wakefulness/sleep, hunger, thirst, sex, and defensive behaviors, among others.

By receiving signals from the hypothalamus, the superior colliculus is thus privy to a host of signals about the internal condition of the organism. Sensory inputs can then lead to motor actions in a way that are appropriate for the animal's state. Is it injured, hungry, sleepy?

Extending the Circuit

We started with the superior colliculus, which receives retinal inputs and can guide movements in a fairly direct way, as some of its connections extend down into the spinal cord and from there can influence muscle movements by way of a single additional connection. We then added the PAG, which helps generate defensive and appetitive behaviors. We considered the substantia nigra, which is particularly important for appetitive behaviors, in a manner that is substantially expanded when we incorporate the striatum, too. We saw that the hypothalamus brings a considerable degree of context dependency to the system (figure 3.6).

Put together, these pieces constitute a sort of "minimal brain," with sensory inputs, motor outputs, and parts in between. Remember that the "in between" is how inputs and outputs get decoupled—no one likes to repeat the same thing over and over, and nature will eliminate anything that does. The overall circuit helps an animal answer the critical question, "Stay, approach, or withdraw?" It helps orchestrate approach and withdrawal actions while an animal navigates challenging environments. The combined

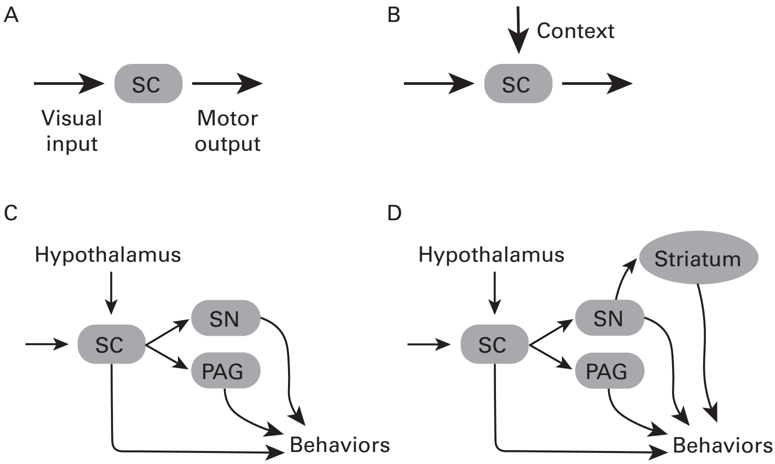

Figure 3.6

Extended superior colliculus circuit (SC). (a) Simple sensorimotor interface, where inputs lead to direct outputs. (b) Context signals can influence the circuit. (c) Connections to the substantia nigra (SN) and periaqueductal gray (PAG). (d) The substantia nigra is also robustly connected with the striatum.

circuit supports an extended behavioral repertoire and frees the animal from responding in the same way every time it receives a specific input.

This mini-brain in the midbrain (and neighboring structures like the hypothalamus and striatum) allowed us to start navigating the central nervous system and considering how some structures contribute to behaviors. To what extent is this exercise of carving out a part of the brain reasonable? Can we separate this mini-brain from the rest, or do we need to consider additional pathways and regions to understand how the mini-brain contributes to behavioral functions? Perhaps the superior colliculus/optic tectum, a key region of this circuit, is sufficiently isolated that such a strategy could work, particularly in "simple" animals. Let's briefly assess this possibility (for a detailed discussion, see chapter 9). In fishes, amphibians, and reptiles, the optic tectum is enormous and wields immense influence (see Striedter 2005). Information processing in these vertebrates heavily includes this area, and its large number of input-output pathways precludes isolating it from the "rest" of the brain in an attempt to understand its functions. Mammals have a forebrain that is rather prominent, including its layered mantle, the cortex. Perhaps in this case the superior colliculus is more isolated and thus a better example of a mini-brain. Au contraire. The mammalian superior colliculus is abundantly interconnected with the remainder of the central nervous system, so much so that one author even suggested that it could help support or even define the "self" (Strehler 1991)—according to the author's logic, the "self" should be located somewhere in the brain that is very well connected anatomically!

This exercise of isolating brain regions and outlining how they contribute to behavioral functions, while useful didactically, is rather unsatisfactory. To some extent, we will continue to resort to it, if only because reading and understanding proceed in a sequential manner. But the reader should remember that we cannot simply point to a brain structure and say that a behavior resides there. Instead, a central thesis of this book is that anatomically *distributed circuits* bring about the behaviors in question. (Even these distributed circuits need to be understood in terms of a fully behaving animal immersed in a broader context.) Bearing this in mind, a potential strategy to appreciate how brain regions contribute to functions and behaviors is to consider the location of interest and a gradually expanding circle of areas to which it is connected. The question is, then: How does this region that we care about help carry out mechanisms of interest *in combination with other regions*?

Before we are able to tackle this problem more directly, we have to build our vocabulary further and familiarize ourselves with many cortical and subcortical areas that have been implicated in domains that a standard textbook would classify as "perception," "cognition," "emotion," and so on. In fact, even before we do that, we need to delve deeper into an issue neuroscientists are faced with front and center: How should we think of individual areas of the brain and their contributions to behavior?

The Entangled Brain

How Perception, Cognition, and Emotion Are Woven Together

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