CONTENTS

CHAPTER 1

Tongue-Tied

Tell me what you eat, and I will tell you what you are.

Taste seems to have two chief uses: 1. It invites us by pleasure to repair the losses which result from the use of life. 2. It assists us to select from among the substrates offered by nature, those which are alimentary.

—JEAN ANTHELME BRILLAT-SAVARIN,
THE PHYSIOLOGY OF TASTE

The nature of pleasure and displeasure have preoccupied humans since the first paleolithic philosophers sat around a fire, roasting meat and talking. What questions could be more essential than "Why do we experience pleasure or displeasure?" Or, "When and why should we allow ourselves to enjoy pleasure or subject ourselves to displeasure?" In the first century BCE, the Roman poet Lucretius offered an answer. He argued that the world was material, composed of atoms and atoms alone. Atoms made up the moon, the fence, and the cat on the fence. They also made up the mouse upon which the cat was

about to pounce. In death, the atoms in the mouse might be rearranged into the body of the cat, but they would continue to exist.[1] In such a world, pleasure was the body's mechanism for fulfilling its material needs. Pleasure led the cat to the mouse. Pleasure was natural; displeasure too. To Lucretius the naturalness of pleasures and displeasures was not a call for hedonism. But it did suggest that a good life could be one in which pleasures were enjoyed and displeasure was avoided. Lucretius recorded his ideas in a moving poem titled *De rerum natura* and typically translated as *On the Nature of Things* or *On the Nature of the Universe*. The poem brought Lucretius's ideas to a large audience. They weren't new ideas, not entirely. In part, Lucretius was reiterating and rewriting the ideas of the Greek philosopher Epicurus. But these ideas were nonetheless given a new clarity and beauty. Yet, when the Western Roman Empire collapsed, Lucretius's words were, bit by bit, lost. By the late Middle Ages, the primary evidence that Lucretius existed was indirect. He could be found in the writings of other scholars, scholars who mentioned and sometimes quoted tantalizingly short excerpts from *On the Nature of the Universe*.

With the fall of the Western Roman Empire, many of the great literary and scholarly works of ancient Romans and Greeks vanished. They were burned, crushed or, more often, simply neglected. Some works were lost permanently. But not all. Many were copied and studied by Muslim scholars in Byzantium; others were preserved in monasteries. Fortunately, Lucretius's poem was among those manuscripts that were saved. In 1417, *On the Nature of the Universe* was found in a German monastery[2] by a restless and curious monk named Poggio Bracciolini.

Poggio was struck by the intense beauty of Lucretius's work. With time, he also became aware that the world Lucretius described, a world full of natural pleasures, seemed to be at odds

with everything he had learned as a medieval Christian. He eventually came to criticize the poem, but not before ordering a scribe to make a copy and then sharing that copy around (and having more copies made). In the coming decades some would come to regard the sentiments embodied in Lucretius's poem as a defining model for the future, grounded in the past. Meanwhile, to others Lucretius's ideas were a threat to Western civilization. Our perspectives on pleasure and the materialism of the world remain as divided now as they were then. Such divisions bubble beneath many of our most politicized debates. We won't resolve such debates here, but we can introduce a missing piece, the answer to the question of why pleasure and displeasure exist. Pleasure is caused by a particular mix of chemicals in the brain. So is deliciousness, the specific pleasure associated with the flavors of food. An animal's body produces those chemicals in order to reward it for doing those things that will aid its survival and chances at reproduction. As Lucretius recognized, this is as true for mice or fish as it is for humans.[3] Displeasure is the opposite. It penalizes animals for doing things that make survival and reproduction less likely. Together, pleasure and displeasure are nature's simple way of helping to ensure animals stay alive long enough to make more of themselves and pass on their genes.

One of the things any animal needs is to eat the right food. Just which food a species needs to be guided to, by pleasure, is predicted by a field of science called biological stoichiometry. *Biological stoichiometry* is perhaps the most boring possible name for a field with enormous consequences for how the world works. It is an obscure field. If you don't study biological stoichiometry, you have probably never heard of biological stoichiometry.

Biological stoichiometry concerns itself with balancing various versions of a single equation. In the simplest version, the left side of that equation is made up of the bodies of organisms that have been eaten (the prey). Think about all of the animals, plants, fungi, and bacteria you have consumed in your own life. The right side of the equation is the body of the organism doing the eating (the predator), along with all of the waste it has ever produced and all of the energy it has ever used. As Lucretius put it, animals "borrow lives from each other."[4] They are relay runners that "pass along the torch of life." Biological stoichiometry deals with the rule by which the baton is passed.

Stoichiometry's rule is that the equation must balance; the nutrients present in the food and those in the consumer (and its waste and consumed energy) must ultimately match. This is where things get trickier, where the problem begins to resemble an elementary school homework question with a man and two dogs on one side of the river and a woman and a canoe on the other. If the body of a predator, for example, has a high concentration of nitrogen, so too must its prey. This seems so obvious as to not even bear writing down. Brillat-Savarin told us this: you are what you eat and you need to eat what you are. But the tricky part is that the equation linking predator and prey relates not just to, say, nitrogen and carbon; it also relates to any other nutrients that the predator cannot make for itself. As a result, the predator and prey must balance with regard to nitrogen but also magnesium, potassium, phosphorus, and calcium, each of which plays a role inside every animal cell.

We can actually write out the proportional number of molecules of each element present in the bodies of different species of animals (and hence the predator, or more generally, consumer, side of the equation). The average mammal, for example, can be described chemically by the list of elements in its body

and their relative proportions. Here is the ingredient list for making a mammal:

$H_{375,000,000}$, $O_{132,000,000}$, $C_{85,700,000}$, $N_{64,300,000}$, $Ca_{1,500,000}$, $P_{1,020,000}$, $S_{206,000}$, $Na_{183,000}$, $K_{177,000}$, $Cl_{127,000}$, $Mg_{40,000}$, $Si_{38,600}$, $Fe_{2,680}$, $Zn_{2,110}$, Cu_{76}, I_{14}, Mn_{13}, F_{13}, Cr_{7}, Se_{4}, Mo_{3}, Co_{1}

Mammals, such as humans, have 375,000,000 times more hydrogen (H) atoms in their bodies than cobalt (Co) atoms. Today, scientists can calculate the elemental ingredient lists of humans and other mammals with great precision. But how do wild mammals know how to find all of these elements in nature in order to have what their bodies need and balance their own stoichiometric equations, equations in which the ingredients they consume match those their bodies need?[5] How does any animal know? How, for that matter, do you know?

For predators that eat their prey's muscles, organs, and bones, hunger (and the pleasure triggered when hunger is sated) might be enough to balance the equation. Dolphins need only hunger and some kind of mental image of what food looks like when compared to non-food (something that tells them not to eat a rock).[6] Things are mostly in balance.

For animals with diets that allow them more choices, things get trickier. For animals that eat plants (herbivores) or animals and plants (omnivores) life is especially challenging. As can be seen in figure 1.1, many elements are found in far higher concentrations in animals than in plants. If an omnivore randomly eats some plants and some animals, it will easily end up with a diet that is deficient in sodium, phosphorus, nitrogen, and calcium. Things are just as tricky for herbivores. How do herbivores and omnivores know how to balance their own stoichiometric equations? To a large extent, they make decisions based on flavor. Flavor is the summation of all of the sensory experiences

that occur inside an animal mouth. Flavor includes aroma, mouthfeel, and also taste.[6] Each of these components of flavor is important in guiding animals toward their needs, but taste plays a special role.

The English word *taste* comes from the vulgar Latin *tastare*, which some dictionaries contend is an alteration of the Latin word *taxtare*, "to handle or grasp." This alteration may be due to the influence of the Latin word *gustāre*, which means to taste. When we taste, we grasp with our tongues. The tongue is covered in taste papillae (the bumps you see in the mirror) in which are found taste buds each of which contains taste receptor cells layered like petals within a flower.[7] These cells are replaced every nine to fifteen days. Even as a vertebrate animal ages, its tongue is always being reborn. Tentacular hairs project from each taste cell. At the tip of these hairs one finds the actual taste receptors, waving in the mouth's tumultuous sea.

Each type of receptor is a like a lock that can be opened only by a specific key. Open the lock with the right key and a signal is sent from the taste receptor along nearby neurons. From there, the signal splits and travels via separate nerves to each of several parts brain. One of the signal's paths reaches the primitive, ancient fish part of the brain that controls breathing, heart rate, and other subconscious, necessary, elements of the body's working. For tastes associated with elements that are needed—such as salt or sugar—one effect of the signal's arrival in this primitive part of the brain is the release of dopamine. Dopamine triggers a flush of endorphins which you experience as a vaguely conscious sensation of pleasure; it is a pleasure that rewards animals for finding what they need. It also creates cravings: "I love this, I want more." Another of the signal's paths reaches the conscious part of the brain, the cortex. Once there,

it triggers the specific sensation associated with what has been tasted, such as "salt," or "sugar."[8]

This taste system works because the elements any particular animal needs are relatively predictable. They are predictable based on the past: what an animal's ancestors needed is likely to be what that animal also needs. Taste preferences, therefore, can be hardwired. Consider sodium (Na). The bodies of terrestrial vertebrates, including those of mammals, tend to have a concentration of sodium nearly fifty times that of the primary producers on land, plants (figure 1.1). This is, in part, because vertebrates evolved in the sea and so evolved cells dependent upon the ingredients that were common in the sea, including sodium. To remedy the difference between their needs for sodium and that available in plants, herbivores can eat fifty times more plant material than they otherwise need (and excrete the excess). Or they can seek out other sources of sodium. The salt taste receptor rewards animals for doing the latter, seeking out salt in order to reconcile their great need and balance their life's stoichiometric equation.

Most mammals appear to have two kinds of receptors that respond to the sodium (Na) in salt (NaCl). One of the taste receptors responds to sodium above a certain minimum threshold concentration. If sodium is present above that concentration, it sends a signal to the brain. Pleasure ensues, as does the conscious perception of "salt." Think of biting into a big soft *laugenbrezel* at the little shop between the airport and the train station in Berlin (or at least that is what we thought of while writing this). This first receptor leads mammals toward salt. For example, elephants walk hundreds of miles to muddy patches of salty soil. In doing so, they wear game trails deep into the ground, trails that trace the geography of their needs.

But as much as not eating enough salt (and hence sodium) is bad, eating too much salt can also be bad. The ingestion of too much salt can easily occur in mammals that live by the sea if they slake their thirst with salt water. To cope with this potential problem, mammals have a second salt taste receptor that detects high concentrations of sodium and, having done so, sends a signal of displeasure and a conscious perception of "too much!" to the brain. If you get a particularly salty bite of your laugenbrezel and feel compelled to brush off some of the salt, it is this second receptor at work. Salt taste receptors lead terrestrial mammals, whether they be mice, squirrels, or humans, toward the concentrations of salt that, on average, they and other terrestrial vertebrates have tended to need over the last tens of millions of years. They lead them toward those concentrations and, simultaneously, away from excess.

Lucretius imagined that fatty foods might be made up of smooth atoms and bitter or sour foods crooked, rough, and barbed ones. They aren't. Instead, the experience any animal has of a particular food reflects how its taste receptors are connected to its brains. The sensation we experience associated with salt, the sense of the taste "salt," is entirely arbitrary. We can know that other animals have salt taste receptors just like our own and we can know that those receptors trigger cravings and pleasure (thanks to detailed studies in mice and rats) and even at what concentrations, but we cannot know what "salt" *tastes* like in those other species. We don't know exactly what the pleasure of encountering such a taste *feels* like in those other species. We don't know anything about the experiences of tastes or pleasures in humans other than ourselves. We just assume they are always the same.

As you can see in figure 1.1, sodium (Na) isn't the only element that is more common in vertebrate bodies, such as those of mammals, than in plants. So too is nitrogen (N). In plants

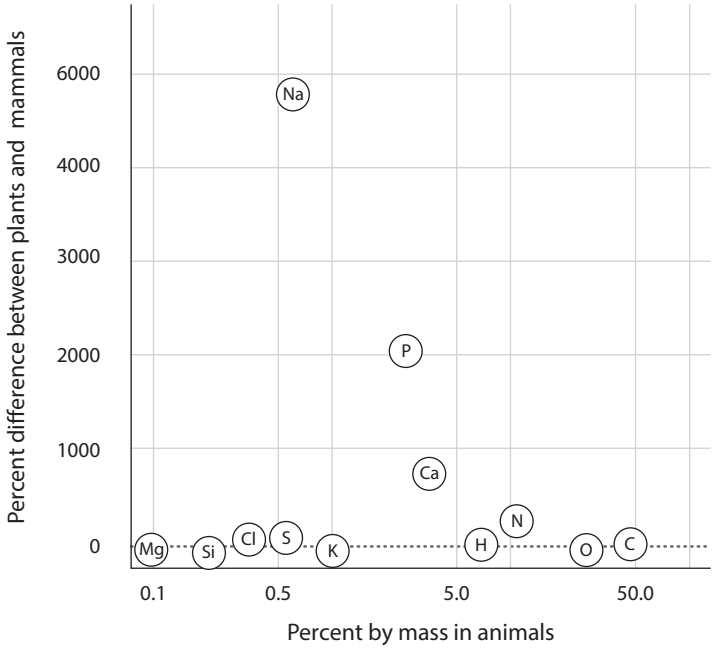

FIGURE 1.1. The percent by mass of the elements most abundant and biologically "essential" in animals (horizontal axis), and how these compare with their abundance in plants (vertical axis). Elements with a positive values are more concentrated in animal than plant tissues. For example, sodium (Na) is nearly 50 times (or 5000 percent) more concentrated in the bodies of mammals than in the tissue of plants. Conversely, silica (Si) is slightly more concentrated in plants than in animals.

and animals, nitrogen tends to be found in the amino acids and in nucleotides. Amino acids are the Lego bricks out of which proteins are made, and nucleotides are the bricks from which DNA and RNA are built.

Animals that eat some plants, be they pigs, humans, or bears, can easily end up with diets deficient in nitrogen. On average, animals have about two times as much nitrogen as plants, as a proportion of their body mass. How do omnivores and

herbivores deal with this shortage? Some species just consume two (or more) times as much food as they need and void the excess. Like aphids, scale insects, for example, drink from the sugary phloem flowing through plant veins. In doing so, they gather the small amounts of nitrogen in what they have imbibed and as much sugar as they need, then excrete sugar water. That excess falls from them and is gathered by ants and some humans as a delicacy. (It is thought the manna of the Bible may have been the excess falling from the tamarisk manna scale insects, *Trabutina mannipara*, feeding on tamarisk trees.) But for mammals, this approach to balancing isn't a great solution. Instead, a taste receptor for nitrogen, or one or another compound that is indicative of foods with nitrogen, seems like a better approach. But until 1907 no taste in humans was known to correspond to the presence of nitrogen, or the amino acids and proteins in which nitrogen is found, in food.

In 1907 Kikunae Ikeda, a chemistry professor at Tokyo Imperial University, was eating a bowl of broth that changed his life. The broth was dashi. Ikeda had consumed dashi before, but on this particular occasion he was struck by its deliciousness. It was salty, a tiny bit sweet and, well, there was a hint of something else, something very good. Ikeda decided he wanted to identify the origin of this extra taste, the very good taste that he would come to call "umami." The word "umami" is rooted in the Japanese words for savory (*umai*) and essence (*mi*). It also means "a delicious taste and its level of deliciousness," as well as "a skillful thing to relish, especially in relation to techniques in art."

The recipe for dashi is superficially simple. It includes fermented fish flakes (katsuobushi),[9] water, and, in some cases, a special kelp (kombu). Ikeda knew the taste did not come from the water. It must then have come from either the fish flakes or the kombu. All Ikeda had to do was identify which compound

in the fish flakes or kombu triggered the taste he believed himself to have perceived, the taste of umami. This was easier said than done. A "simple" dashi broth can contain thousands of chemical compounds potentially able to produce tastes or aromas. Ikeda had to identify these compounds and test them one by one. According to the tally of Jonathan Silvertown in his book *Dinner with Darwin*,[7] it took thirty-eight separate steps to finally extract some gritty crystals from the kombu kelp in the broth that appeared both to be relatively pure (a single compound) and to taste of umami. The crystals were glutamic acid. Glutamic acid is an amino acid; it is a building block of protein and so a reliable indicator of the presence of nitrogen in a food. The taste of umami is a taste that rewards us for finding nitrogen. Umami taste, triggered by glutamic acid, leads us toward our necessary amino acids. But umami taste is not triggered by glutamic acid alone.

Subsequent studies by other Japanese researchers would show that in addition to glutamic acid, inosinate and guanylate, two ribonucleotides, can also trigger umami taste. These two ribonucleotides are not found in the dashi's kombu, but instead in the fish flakes. When inosinate or guanylate and glutamic acid are experienced together, they produce a kind of super umami. Glutamic acid and inosinate are experienced together in dashi. Dashi is rich with super umami, a flavor that is both deeply pleasing and indicative of the presence of nitrogen.

For decades, few scientists outside of Japan believed Ikeda's result (nor, for that matter, the subsequent results related to inosinate and guanylate). But don't feel too bad for Ikeda; he patented the method used to produce MSG in 1908. MSG results from the combination of glutamic acid and sodium. Thanks to that patent, Ikeda did just fine for himself.[8] People were willing to pay for umami taste even before they believed it

to exist. As for why Ikeda's work was neglected outside of Japan, it was partly because the first paper was written in Japanese and so not widely read by scientists in Europe and the United States. But it wasn't just language, it was also a problem of mechanism. Although Ikeda could show that when his glutamic acid crystals were added to a food that they improved its taste, he hadn't identified how the mouth tasted them. The taste receptor for umami would not be discovered for ninety years. The separate receptor that responds to inosinate and guanylate would take even longer to resolve. It was only once they were discovered that umami taste was widely accepted by most sensory scientists as a human taste.

If you return to figure 1.1, you will see that another element that is much more common in animals than in plants is phosphorus (P). Phosphorus is more than twenty times as concentrated in the bodies of animals as in the tissues of plants. A lack of phosphorus is a key challenge faced by many animal species.[9] Why then isn't there a taste receptor that detects phosphorus in food and rewards animals for finding it? One possibility is that foods, particularly foods in the form of whole animals with lots of nitrogen, typically also have sufficient phosphorus. Perhaps having a receptor for one of the two nutrients was sufficient. Nature often packages nitrogen and phosphorus together. Yet, this wouldn't explain how herbivores or even most omnivores find phosphorus. Another possibility is that some animals do have a phosphorus taste receptor.

Michael Tordoff is a scientist at the Monell Chemical Senses Center (in the world of taste, all roads lead to Monell). He has specialized in laboratory studies of poorly charted tastes, including the taste of phosphorus. Since the 1970s, studies have shown that mice are able to somehow taste phosphorus salts. More recently, Tordoff was able to show that mice appear to be

able to distinguish between low concentrations of such salts (which please them) and high concentrations (which displease them).[10] Tordoff suspects that most mammals, including humans, have the ability to taste phosphorus salts and to distinguish pleasing concentrations of such salts from displeasing ones.[11] With the discovery of umami, the broad acceptance that umami was a taste required the discovery of the taste receptor for umami and its functioning. Tordoff is on his way to that step with phosphorus. Recently he even discovered what appears to be the receptor that alerts mice that they have found too high of a concentration of the phosphorus (in the form of phosphates).[12] No one has yet discovered the receptor that tells them when they have found just the right amount. It is possible that someday soon phosphorus may be accepted as an additional human taste.

You might imagine that the discovery of a new taste, a taste that you might be experiencing each time you eat, would trigger hundreds of follow-up studies. An award of some sort. Television interviews. It hasn't yet. The world is full of mysteries. Even mouths are full of mysteries. As a result, Tordoff's studies of the taste of phosphorus are cited by relatively few other papers. One of those papers demonstrates that cats, like mice, prefer foods that contain more phosphorus. Phosphorus is now added (as phosphate) to most cat foods to encourage cats to eat the food. Cats don't need to believe or not believe Tordoff's results in order to experience the pleasures, it seems, of phosphorus taste. Meanwhile, the other element that is scarce in animal diets relative to animal bodies is calcium. Tordoff thinks he has discovered evidence of a calcium taste receptor too.

Most of the elements and compounds we need in our diets are necessary for building new cells and other components of our bodies. Because of this, we need them in proportion to their

relative rarity or abundance within our bodies (that equation again). In addition, however, our bodies also need energy for daily activity; even once the building is built you have to keep the lights on. The more active a species is, the more such energy it needs. This is as true for insects as it is for mammals. The most active, aggressive, ants, for example, require the highest calorie diets.[13] Most of that caloric energy, whether for ant or elephant, comes from breaking apart carbon compounds.

Simple sugars, all of which are small carbon compounds, are easy for animals to convert into energy. Simple sugars include glucose, fructose, and the result of their biochemical marriage, sucrose. Sweet taste receptors reward animals for finding these sugars.[10] They reward us with sweetness for eating mangos, honey, figs, or nectar. Complex carbohydrates, such as starches, are also sweet to many mammals. Old world monkeys, apes, and humans are unusual in that their sweet taste receptors do not respond to starch. However, these species produce an enzyme called amylase in their mouths. This amylase does not aid in the digestion of starch (which happens later) but has been hypothesized to break down some of the starch in the mouth so that it can be detected by the sweet taste receptor. Ancient humans, like modern gorillas or chimpanzees, produced some amylase in their mouths but not much. However, with shifts to more starchy diets, some groups of humans evolved the ability to produce more amylase in their mouths, perhaps to more quickly perceive starch to be sweet. Evolution can make bland foods sweet and vice versa, simply by changing how they are perceived.

The other source of energy for working cells is fat (protein can also be converted to energy, but is the body's last choice). Fats contain twice as much energy per gram as do simple sugars. Not surprisingly, many mammals appear to experience pleasure

in eating fat. For example, Danielle Reed (yet another scientist at the Monell Chemical Senses Center) used to give her laboratory mice a high fat diet. When she did they would, as she put it, go on a "Friday night binge. They would just eat all their fat and groom their hair with it and they'd just get in the middle of their fat. They love fat."[11] Surprisingly, it is not clear what it is about fat that mice or other animals enjoy. The answer may be mouthfeel. Fats have a pleasing mouthfeel (a gastronomic term for the sensation of touch as it is manifest inside the mouth). Put a piece of avocado in your mouth. It will be pleasing, but the pleasure is not the taste (it is not very sweet, nor sour, nor salty, nor really umami). Nor is the pleasure of the avocado its aroma, which is simple, often described simply as "green." The pleasure is, instead, the feel, the smooth touch of the fruit, the same smoothness we experience when enjoying butter or cream. This touch is part of the story.[12] But mysteries remain.

Salty, umami, and sweet taste receptors (and maybe also phosphorus and calcium taste receptors) evolved to point animals, through deliciousness, to what might otherwise be missing from their diet, whether in order to make new cells or, in the special case of simple sugars, to make new cells and to run them. But taste receptors can also serve the opposite purpose; they can point animals away from danger. They do so through feelings of displeasure. In some contexts, sour taste, which detects acidity in food, is displeasing. We will return to why this might be in chapter 7 (sour taste is mysterious and yet potentially very important to our human story). The more clear-cut case is that of bitter taste receptors. Bitter taste receptors allow animals to identify plants, animals, fungi, and anything else in nature that might be dangerous to ingest. For nearly all taste receptor types, animals have one or two (salt) basic classes of receptors. With bitter taste receptors, animals have many kinds.

Each kind of bitter taste receptor is triggered by one or more chemicals or classes of chemicals. Lucretius wrote of "nauseous wormwood," a key ingredient in absinthe, whose "foul flavor set the lips awry." We now know that it is the absinthin in wormwood that triggers one of our bitter taste receptors. And we even know which receptor (hTAS2R46, if you are curious). A different receptor responds to strychnine in plants; another responds to the noscapine found in poppies and their relatives. Yet another responds to the salicin in willow bark (and aspirin). Because being able to avoid toxic chemicals is very important (and failing to do so often results in having no offspring and so not passing on your genes) bitter taste receptors tend to evolve relatively rapidly. Species tend to have bitter taste receptors that reflect the dangerous kinds of compounds they are most likely to find in their environments. Humans and mice, for example, have about 25 and 33 kinds of bitter taste receptors, respectively, but the overlap between ours and theirs is modest.[14] Some compounds that mice evolved to avoid (and hence taste as bitter) have no taste in our mouths and vice versa. Variation even exists among humans within populations. As Lucretius put it, "what is sweet to some, to others proves bitter." As a result, a group of people might be able to detect more kinds of compounds as bitter than any individual. The combined knowledge of a community contains three types of bitter compounds then, those that everyone tastes as bitter (dangerous), those that some people think are bitter (maybe dangerous) and those that no one tastes as bitter (safe).

But, although most vertebrate species can detect many kinds of potentially toxic compounds via many types of taste receptor, and different individuals are able to taste different compounds as bitter, individual vertebrates perceive only one kind of bitter. All the bitter taste receptors are wired to a single nerve

and only register a single conscious perception BITTER.[13] If a bitter compound is ingested in a high concentration, it can trigger nausea. If it is ingested at a high concentration twice (for example, via two gulps) the stomach muscles of the consumer stop contracting in rhythm. They begin to twitch out of sync which ultimately, if the dance of indigestion is sufficiently strong, triggers vomiting. Bitter taste receptors tell us things are bad and then, with vomiting, trigger both a reminder that they were serious and, with that reminder, expel some of the offending compound.

The displeasing sensation a species experiences in association with bitter compounds is just as arbitrary as that of saltiness or sweetness. Its key message is simply displeasure, displeasure that, like a stick, is meant to lead animals from things they are too stupid to avoid otherwise.[14] As humans we have learned to sometimes ignore the bitter taste warning these receptors offer us, such as when we drink coffee, hoppy beers, or bitter melons. We do so even as our tongues cry out, "Bitter. Danger. Bitter. Danger." "Hush now," we say to our tongues as we enjoy coffee, tea, or hoppy beer. "Hush, I know how much of this toxin I can consume without danger. Hush, I know what I am doing. I have learned."

What we've just described of the taste system is representative of the average terrestrial vertebrate. But as terrestrial vertebrates have evolved, their lifestyles have changed. Such changes have led to (or in some cases been caused by) evolutionary changes in taste receptors, such that each species perceives, with its mouth, a different world. Or, as Lucretius put it, "there are different senses in living creatures, each of which perceives in itself the object proper to it."[15] Some of the changes are subtle and relate to the thresholds at which particular compounds are detected. Others of the changes are more extreme and include the losses of entire tastes.

TABLE 1.1. Taste Thresholds for Humans

Taste	Substance	Necessary concentration to trigger response (parts per million)
Salty	Sodium chloride (NaCl)	2000 ppm
Sweet	Sucrose	5000 ppm
Umami	Glutamate	200 ppm
Sour	Citric acid	40 ppm
Bitter	Quinine	2 ppm

The minimum concentration of a substance needed to trigger a taste receptor varies greatly from receptor to receptor. Bitter taste receptors tend to be triggered by even very low concentrations of the chemicals to which they respond, such as quinine, a toxin produced by plants. These receptors evolved in order to warn us away, and that works best if it happens before we ingest a lot of whatever it is that has touched our tongue. Sugar, on the other hand, is most useful if it is in high concentrations. Below such concentrations our tongues don't even know they've encountered something sweet. The other taste receptors fall in between. Sour is the most unusual of the taste receptors. It deserves special treatment so we'll return to it in chapter 7. The data shown here are for a subset of studied humans. These thresholds, however, differ among species as well as among individual humans.

Perhaps the fastest of the slow ways taste receptors evolve is by breaking. Taste receptor genes tend to be large and so are prone to collect mutations that break them so they can no longer function. Over millions of years the genes for particular taste receptors have broken again and again when the desires (or avoidances) of an animal and its needs are mismatched. Cats, be they pumas, jaguars, or house cats, are strict carnivores (though see, in chapter 4, the special case of cats and avocados). Cats have evolved specialized forms of hunting so as to be extraordinarily good at killing their prey. If you look again at figure 1.1, you will see that an animal that only eats other animals will tend to have in its diet about the right concentration of nitrogen and phosphorus. It also ends up with enough energy, in the form of fat and sugars in its prey's cells, to carry out its daily activity. Cats with sweet taste receptors are no more likely than those without to survive and flourish; if they spent too

much time sipping nectar and too little time eating prey they might have even been less likely to survive. As a result, when the sweet taste receptor of an ancient cat broke, that cat survived nonetheless. It did more than survive, as Xia Li (at the time also a researcher at the Monell Chemical Senses Center) recently showed. It begat all modern species of cats. No modern cat species have functioning sweet taste receptors.[15] Forests of sweet fruits and nectar are not delicious to cats, not even a little. If you give a cat a sugar cookie, well, it really doesn't care. It does not experience any pleasure in the cookie's sweetness; the cookie, to the cat, is not sweet.

Like cats, other carnivores such as fur seals, Asian small-clawed otters, spotted hyenas, fossa, and bottlenose dolphins also have broken sweet taste receptors. All of these breaks in the sweet taste receptor gene occurred independent of each other; they are convergent forms of falling apart. One question one might ask about these carnivores is why others of their taste receptors haven't also broken. Cats are unlikely to need more salt than their prey contain. That the cats' salt taste receptors, as well as those of other carnivores, haven't also broken may just be a matter of time. Sea lions have broken sweet taste receptors and broken umami taste receptors. Dolphins have taken this trend further. They no longer taste sweet, salty, or even umami.[16] They thrive on the basis of hunger and satisfaction alone, hunger, satisfaction, and the belief that anything that moves like a fish is dinner. This raises the question of just what it is about a prey item that pleases a dolphin. We don't know. The pleasures of dolphins, whatever they are, are beyond the understanding of science, at least for now.

The loss of particular taste receptors is not the unique purview of predators. Losses have also occurred in animals with diets that are specialized in other ways. The ancestors of giant

FIGURE 1.2. Giant panda surrounded by its one true delicacy.

pandas were bears. As bears, they were omnivores, drawn to living prey but also sweet berries and sour ants. But giant pandas evolved to take advantage of a new diet, one dependent on bamboo. On bamboo alone, they thrive. Initially, as they shifted to bamboo they enjoyed both the bamboo and meat. But with time, giant pandas that were still drawn to meat were either no more likely to survive and mate, or, even less likely, their wants and needs mismatched, their attention distracted. With time the umami taste receptors of giant pandas, like the sweet taste receptors of cats, broke.[17] Now, even if offered meat, giant pandas decline.[18]16

It is unlikely that the descendants of cats, sea lions, or dolphins will enjoy sweetness even long into the future, nor will giant pandas enjoy savory tastes, even though their preference for bamboo has led their populations to decline, in lock step, with declines in size of bamboo forests.[19] It is harder to make something from scratch when it is needed than to break it, a

lesson from evolution for daily life. Harder, but not impossible.

Sweet taste receptors, for example, have been lost, but they have also been regained. The ancestor of all modern birds, mammals, and reptiles lived about three hundred million years ago. That ancestor appears to have been able to taste salty foods, savory foods, and sweet foods. However, the ancestor of all modern birds lost its sweet taste receptor. For reasons that cannot yet be discerned, the sweet taste receptor was no longer useful. As a result, birds cannot detect sweetness. Or at least most birds can't.

Hummingbirds descend from ancient swifts. Like modern swifts, these ancient swifts were exclusively insect eating. The ancient swifts were pleased by umami tastes, such as those associated with the bodies of insects or worms, but disinterested in sugars. However, roughly forty million years ago, one population of swifts began to feed on nectar and other sugar sources, perhaps simply to slake their thirst. The nectar was not sweet to the birds. To the extent to which it tasted like anything, it tasted like water. But unlike water, the nectar provided sugars. It has been hypothesized that individuals that drank more nectar were more likely to get energy and pass along their genes, so much so that their umami taste receptor evolved so as to be able to detect sugars in addition to the compounds that ordinarily trigger umami taste (amino acids such as glutamic acid as well as some nucleotides). This swift lineage would become the first hummingbird. Hummingbirds, unlike most birds, can taste sugars and amino acids. However, because they do so using a single receptor it is likely that they experience the two substances as the same, pleasurable sensation, sweet-umami.[20]

These examples of the ways in which an animal species can come to find new things delicious and, in doing so, remedy its

deficiencies, are beautiful. They are the fine tuning of the ability of organisms to satisfy their needs through pleasure. The more we study the evolution of taste receptors, the more these stories seem to emerge. We can even predict where they might occur. Hummingbirds are not the only birds that feed on nectar. Sunbirds, flower-piercers, and honey-eaters are unrelated to hummingbirds, but they also feed on nectar and other sweet foods. It seems likely that they too have evolved the ability to detect sugary foods and be pleased by them. Three different desert mammals, in different deserts, have evolved the ability to feed primarily on plants that exude salt. Doing so required them to evolve extraordinary traits that make this lifestyle possible, such as hairs in their mouths that help to scrape salt from the plants. These salty-plant-eating mammals have no need to seek out extra salt and so it seems likely that they have lost their salt taste receptors.[21] But all this fine tuning raises an interesting question when we consider our own lineage.

We are primates, which is to say we are related to lemurs, monkeys, and apes. Within the primates, our narrower branch is that of the hominids, which includes us as well as gorillas, chimpanzees, bonobos, orangutans, and an entire zoo of extinct relatives. Within the hominids, we are the sole surviving member of the tribe Hominini, the hominins. If we look across the entirety of the primates, species differ greatly in their taste receptors. They differ both in what their receptors detect and the thresholds at which they detect them. Some plants that are bitter to us (and deadly) are not bitter (nor dangerous) to some of the monkeys, for instance. Additionally, while we appreciate foods with a relatively low concentration of sugar to be sweet, marmosets only perceive foods to be sweet if the sugars are highly concentrated. In other words, comparing species across the entirety of the primates we see differences, some of them

quite big. But then here is the curious thing. If we compare ourselves to our closest living relatives, the chimpanzees, our taste receptors are actually very similar to their taste receptors. What is delicious to a human is, for the most part, delicious to a chimpanzee. This is surprising since, in the time since our shared ancestor, we and chimpanzees have embarked on radically different culinary paths. Chimpanzees live in the forest and, to a lesser extent, grasslands, and eat fruit, insects, and the occasional leg of monkey. We colonized nearly all of terrestrial Earth. As we did, we came to eat something different in each new habitat. Why hasn't the difference between our diet and that of chimpanzees precipitated some kind of major change in taste receptors? In part, the answer is that there have been some subtle changes, if we look closely enough. But there is something else.

When our ancestors began to develop culinary traditions and tools, they found ways to take the foods of any habitat and alter them so as to make them more delicious. In doing so, they dulled natural selection's effects on their taste receptor genes. They dulled nature's effects on which versions of such genes were passed one generation to the next. Our ancestors did not have to wait for natural selection to solve dietary deficiencies through the differential survival and reproduction of individuals with more locally relevant taste receptor genes. They compensated for bland diets by using tools to seek out flavor. Those flavors were often (though not always) indicators of what they needed. This is what Lucretius might have called a "swerve." Through a modicum of consciousness and a pinch of free will our ancestors altered their situation. In doing so they changed the world. In seeking deliciousness, they caused a swerve in the story of their kind, of our kind. This swerve, as we'll argue in the next chapter, was a key step in the evolution of our ancestors.

They figured out how to make tools to find foods that were tastier than those that were otherwise available. They used tools to make their habitats more delicious, then they used tools to help make the landscapes wherever they traveled more delicious. In this way, the pleasure of deliciousness was central to human evolution.[17]

INDEX

A page number in *italics* refers to a figure or table.