SENSATIONAL

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The Social Lives of Animals

SENSATIONAL

A New Story of Our Senses

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My senses sing their song of you. The sight and sound
of you are its lyrics, the melody your scent and touch.
Your harmony enfolds me; you are my world.

– *Punkin*

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Introduction

Light, shadows and colours do not exist in the world around us.

– Presentation Speech by Professor C. G. Bernhard, Member of the Nobel Committee for Physiology or Medicine

It's a glorious spring morning in Sydney and I'm full of nervous anticipation as I cross the university campus, heading toward the lecture theatre, where I'm going to be talking to the latest group of students about the senses. I love to watch their faces when I describe the wonders of sensory biology. It's an amazing topic and I want to do it justice; I'm not just relaying information, I'm giving a performance in the hope that my enthusiasm might kindle theirs.

On my way, I cut through a Sydney landmark known as the Quadrangle, the centrepiece of the university campus. The architects added a finishing touch, a subtropical tree, in one corner; each year, as the Southern Hemisphere spring takes hold, this venerable jacaranda tree erupts into bloom, its fragrant lilac flowers calling time on the academic year. Jacarandas across Sydney join in, transforming the city. For a month, the parks and pavements are blanketed with petals. For me, it's the sensory highlight of the year.

As I admire the grand old tree, I can't help pondering how incredible it is that photons of light and molecules of smell weave such majesty. How does my brain access this basic information and transform it in the greatest of all synergies to a perceptual experience?

Though my attention is captured by the jacaranda, I'm aware of a host of other sensations. An Australian magpie is calling from a perch atop one of the buildings that surround the Quad. Its burbling, oddly metallic call sounds like a steampunk version of the songbirds that I grew up with in England. At the same time, I can feel the morning breeze coming in from the Pacific Ocean through the archway on the east side of the Quad. My mouth is filled with the warming flavour of one of the aniseed lozenges that I rely on for a clear voice in each lecture. At the same time, a combination of other senses keeps me upright, while updating my brain on my bodily needs, and keeping me alert to my surroundings.

And this is just a fleeting moment of sensation. The changing stream of sensations provides our perceptual link to the world, a multiplicity of incoming messages that come together to write the autobiography of every second of our lives. For all that our perception seems like a coherent, singular sensory experience, it's a harmony of many distinct, yet compounded, senses. The question of just how many senses still lacks a definitive answer twenty-three centuries since the first reasoned attempt was made.

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The Greek philosopher, Aristotle, is justly regarded as one of the most influential thinkers in history. Sometimes his ideas didn't quite hit the mark, for instance his assertion that bison discourage chasing dogs by firing caustic turds at them, or his intriguing idea that bees are deaf on the basis that he could see no ears. Notwithstanding the occasional misstep, his legacy is extraordinary. It's been said that the science of biology sprang from his labours and many things that he described over 2,000 years ago have stood the test of time. Indeed, it was Aristotle who is credited with the discovery, if that's the right word, that we have five senses (or, more formally, sensory modalities): vision, hearing, taste, smell and touch. Often, Aristotle gets a bad rap for this, largely because it seems to state the bleeding obvious. In his defence, this was only a small part of his insightful and ground-breaking theories about perception and how the senses combine to provide us with our experience of the world. Nonetheless, poor old Aristotle's name is typically drawn into the fray any time the question is asked: 'how many senses do we have?'

This rule of five is still the basis for our early education in the senses, yet it's some way from the whole story. We certainly have more than five and depending on how we slice and dice the different categories, we might have as many as fifty-three. Touch, for instance, is a composite of multiple different senses that could be subdivided, then there are others such as equilibrioception (the sense of balance) and proprioception (our sense of our body's position) that lie outside the original five. Putting a precise number to the senses, though popular as a quirky topic of debate, isn't especially helpful. Nevertheless, it's important to know what we mean when we describe something as a sense.

Generally speaking, a sense can be defined as a faculty that detects a specific stimulus by means of a receptor dedicated to that stimulus. For example, when light enters our eye, it is absorbed by a molecule known as a retinal, which is found within the light receptor cells of the retina. The light's energy causes the retinal to perform a tiny molecular contortion, in turn setting off a chemical chain reaction that ultimately produces a minute quiver of electricity. It's this tiny zap that gets transmitted along the optic nerve to the waiting brain, which interprets the message and countless others that arrive simultaneously from neighbouring receptors to provide us with the visual sensation of the light. This process of converting a stimulus into a signal that the brain can understand is known as transduction.

Taste receptors, meanwhile, coat our tongues, the inside of our cheeks and the very top of the oesophagus. Give them a molecule and milliseconds later, they'll be telling the brain all about it. We also have taste receptors sprinkled around the body in places such as the liver, the brain and even the testes. This latter revelation, from a paper published in 2013, gave rise to a fad among young men to dangle their balls in such things as soy sauce, with some even claiming to have registered a savoury hit. The thing is, though taste receptors may be found in such extraordinary places, they're not organised into taste buds and nor are they wired to the brain in quite the same way as the receptors in our mouths, so they don't deliver the experience of flavour. The net result is that the participants exposed themselves not only to condiment-covered gonads but to accusations of wishful thinking. Notwithstanding the bowls of ruined soy sauce, a sense is only a sense if it involves not only specialised receptors, but a functioning information highway to the brain's sensory cortex. Yet though the nervous pathways of our senses lead inexorably from receptors to brain, it would be wrong to conclude that the brain is merely a computer, neutrally receiving and decoding input.

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The brain is the seat of all your knowledge, emotions and personality; it's the home of your innermost thoughts and the place where you experience everything in your life. Situated safely within the protective capsule of the skull, the brain sits in a carefully controlled physiological equilibrium. It has no sensations of its own, yet this is where all our experiences occur. Supplied by a vast and complex network of connections to the sensory organs, the brain receives the equivalent of terabytes of information every second. It processes and interprets all of this information almost instantaneously, meshing together input from different sources in a seamless computational feat that has no equal. The result of all the work that the brain does in sifting, ordering and processing the incoming information is known as perception. But this is a far from passive process. The brain doesn't simply collect and organise data, it actively regulates and conditions. Signals from the outside world are interpreted and layered with biases, prior expectations and emotions. This integration of sensations and sensibilities plays a powerful role in our perceptions.

Many years ago, on the only occasion that they set foot outside of Britain, my grandparents travelled to Vienna. It had always been my gran's dream to visit there, to revel in the beautiful city, to see its architecture, to taste Sachertorte, to hear the famous waltzes in their birthplace. Later she recounted how they'd rounded a building and come across the famous river that bisects the city.

'Look, Jim! The Danube!' she called out in her excitement. 'They say that if you're in love, it looks blue!'

My grandad wasn't a man easily stirred by poetry. His Yorkshire vowels as flat as the cap that he habitually wore, he replied tersely, 'Looks bloody brown to me.'

While common sense might dictate that the waters of such a major, industrialised river would not ever resemble an azure, sylvan pool even to the most hopeless romantic, there is a nugget of truth to this. When we're emotionally aroused, activity increases in the brain's visual cortex and what we see becomes richer and more brilliant, even if not necessarily bluer. As for my grandad, his sensations on that trip were likely guided by his attitudes. Our mindset, to some extent, influences neural activity in our brains so that we see what we expect to see.

Ultimately, the convincing perception of reality that we each enjoy is actually a complex but brilliant illusion. This, more than anything else in discussions of the senses, causes people to baulk. We think of ourselves as rational, discriminating creatures, so how can our immediate experiences be illusory? To illustrate this, we can use a simple example. I have a mug of tea in front of me as I write. If I were to ask someone to inspect it closely and describe it, they might tell me the colour of the mug and its contents, that it smells of tea, that it's hot. If they took a sip, they might tell me that it tastes slightly bitter, milky, and overall, well, like tea.

Their experience of my mug of tea would seem entirely and objectively real to them, and they'd take their reality to be identical to mine. Yet while our sensory experiences of the tea would overlap extensively, the overlap wouldn't be complete. Our appreciation of the subtleties of colour might differ. Likewise, the smell and taste of the tea would be different for each of us. If the other person had recently come in from the cold, the tea would feel warmer to them.

In addition, our feelings colour our perceptions. Perhaps the other person is from the Middle East and is appalled at the idea of putting milk in tea. If this were so, their response to the mug of tea would be shaped, in part, by their cultural judgement. The experience feels real to each of us, yet no experience is objectively correct. That doesn't stop people trying to argue that their subjective perception trumps that of others.

This shading of different realities is only the start of the great illusion. It gets more fascinating, and much weirder. It's one thing for people to allow that there might be an alternative perspective on colour, for example, but it's quite another for people to accept that colour doesn't actually exist outside of our brains. Not only is there no colour, but there's also no sound, or taste, or smell. What we perceive as red, for example, is just radiating energy with a wavelength of around 650 nanometres. There's nothing intrinsically red about it; the redness is in our heads. What we think of as sound is just pressure waves, while taste and smell are no more than different conformations of molecules. Although our sense organs do a splendid job of detecting each of these, it's the brain that construes them, converting them into a framework for us to understand that world. Valuable though this framework is, it's an interpretation of reality and, like all interpretations, it's subjective.

The seamless conjoining of all our sensory information into a single, integrated experience is no mean feat and to achieve it, the brain relies on a little trickery. For instance, it has to compensate for discrepancies in the time it takes to process the different senses: vision, being so data rich, takes a fraction longer than the other senses. That's why even in the twenty-first century we begin sprint finals with a starting pistol, rather than traffic lights. The fact that a pistol is used isn't about tradition, some anachronistic nod to our frock-coated forebears, it's simply because athletes, like the rest of us, are slightly slower to react to the light than the sound. Our sensory synchronisation is only possible because the brain imposes slight lags on different senses to make everything line up. Moreover, everything we experience has already happened by the time we register it. To keep up with the real world and to compensate for this slight delay, the brain has to predict movements. If it didn't, we'd be hopelessly out of sync and clumsy.

With so much information flowing in, demanding immediate attention, how does the brain manage to keep up with it all? The answer is that it doesn't. It filters and winnows the information in its perpetual quest for what's important. It's especially attentive to novelty and change; most of the sensory information that we constantly gather never make it past the periphery of our attention into our consciousness. If you're sat down now, you're not likely to have registered the pressure of the chair against your back, or the clothes against your skin – at least until you read this sentence. This isn't the brain being lazy, but rather it's just separating the important from the irrelevant. The downside is that the brain often misses subtleties, which is how dextrous magicians manage to fool us so consistently.

This illustrates the bottleneck between sensation and perception, between collecting information and processing that information to the point that we become consciously aware of it. This is particularly important in vision. The brain seeks patterns and cuts corners by using a template, known as the internal model, of what it can expect to sense based on its experience of what it has sensed before. This can be incredibly useful in that it allows the brain to work with incomplete data, conjuring a full picture from fragments.

However, it's also the reason that we're subject to illusions, and vision in particular is subject to being fooled. Take for instance the well-known film of the rotating theatrical mask. As we watch the mask slowly revolving, we might first see the convex surface of the mask and that's easy; faces are the human brain's bread and butter and everything makes sense. But what happens when we see the mask's concave side? The brain turns it inside out, so we invariably see it as convex surface, like every face we ever see. Even though we know that what we're seeing is hollow, the brain's internal model overrides our reason.

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The dominant role played by the brain in perception means that we might envisage it as the conductor of our sensory orchestra, coordinating and integrating the separate inputs into a coherent, rich single experience. But without an orchestra, there's no point to a conductor. The brain exists only because there is sensory information to process. In answer to the age-old question of 'which came first?', the senses are the egg to the brain's chicken. Indeed, plenty of organisms get by without a brain, yet many of those can still perform basic sensing. Imagine a bacterium, far smaller than can be seen with the naked eye, seeking nutrients amid the expanse of a cup of water. Its hair-like whip of a tail spins, describing microscopic circles that push it along like a boat's propeller. The bacterium has no goal in mind, but it can detect chemicals in the water and follow them to their source. It locates a faint trace of sugar, a welcome meal for a hungry traveller, and moves toward it. As it approaches, however, it senses a new chemical, a protein, that indicates trouble in the form of another organism. Reflexively, the tail spins again, this time in the opposite direction and the bacterium changes course. This story of how bacteria such as *Escherichia coli* track nutrient gradients is simple, yet it describes the operation of something fundamental: the very first sense to emerge.

Life evolved in water some 4 billion years ago. The first organisms were static, unable to move except with the assistance of currents. Staying exactly where you are isn't the most satisfactory arrangement, however. The ability to seek out pastures new allows an adventurous microbe the chance to exploit new and untapped resources. Cyanobacteria, among the first life forms to appear, achieve their ambitions of mobility in various ways. Some squirt out little jets of slime to propel themselves. Bacteria glide, crawl and swim as a means to relocate. Mini migrations such as these are much more effective if organisms are able to navigate. Chemical gradients are one property of the physical world that provides them with their bearings. Light is another. Photosensitive proteins, such as rhodopsin, absorb light and as they do so, they undergo a chemical reconfiguration that is the basis for detecting the sun's rays and the sustaining energy that they provide.

These foundational steps in the evolution of complex, sensory life were accompanied by another – the ability to detect changes in pressure, otherwise known as mechanosensitivity. Bacteria have channels in their outer membranes that open in response to pressure. Essentially, these are what stops them bursting after overdoing it on the pudding, they're what allow the bacteria to match the pressure of their inner selves to the outer world. It's been speculated that these sensitive channels were the forerunners of our own, more elaborate mechanosensation. Certainly, by the time we get to more sophisticated organisms, for instance Protists, like *Paramecium*, we can see that they respond to touch. Like bacteria, *Paramecium*'s entire body amounts to just one living cell, but giving it a gentle tap causes its internal pressure to change and it responds by zipping away in the opposite direction. Incredibly enough, this simple riposte to mechanical stimulation is what eventually gave rise to hearing and touch, just as light detection was the starting point for vision, and bacteria's ability to track chemicals ultimately yielded our senses of smell and taste. These advances occurred billions of years ago in the simplest creatures and it's a sensory legacy that has been passed down to each and every branch of the tree of life.

Across evolutionary history, organisms have climbed a sensory ladder, with each new rung offering an extraordinary advantage to those that ascended it. The crucial currency for these advances is information: about the environment, about predators and prey, about competitors and potential mates. Our senses were bequeathed to us by ancient organisms following gradients in a primeval swamp, and ultimately these senses were the driving force behind the evolution of the brain.

In fact, the normal workings of the human brain depend on sensory inputs and in the absence of these, strange things start to happen. Recently, I visited a sensory-deprivation chamber in Sydney's eastern suburbs. For the most authentic experience, I was told, I'd need to be fully undressed, to avoid the sensation of clothing against my skin, which might put a barrier between myself and the bliss that awaited. And so it was that I found myself stark naked and self-consciously stepping into an egg-shaped pod, before pulling the lid closed and embracing sensory oblivion. I lay down, my weight supported by a shallow pool of super-saline water at the same temperature as my blood and with ear plugs to still the faint noises from without.

At first, my main emotion was a kind of fretting boredom, my mind chiding me like a fractious child for the withdrawal of stimulus. Once that passed, it switched to stand-by and I relaxed, but in the absence of anything to see, my mind started to conjure things – flashes of light, geometric patterns that fizzed to life and then shrank to nothingness. This is formally known as the Ganzfeld effect, or more evocatively, 'the prisoner's cinema'; it's been experienced by miners trapped in the dark underground, and by polar explorers whose entire visual field may consist of a uniform white. In Ancient Greece, there are records of philosophers descending into caves to induce these hallucinations, in the hope of gaining insight. Given time, the light show can sometimes develop into more fantastical waking dreams. Underlying all of this is the brain's frantic efforts to build its internal model, even though the sensory information it needs to construct that model has been cut off. The results are odd, though to some they can feel disturbingly real. In normal life, for most people, this internal model provides the brain's sensory framework, an illusion that it augments and updates as information comes in. It's this fantasy that paradoxically provides our experience of what we call reality.

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But what is reality, and more generally, what does it mean to be alive? However we might try to answer this, it's fair to say that even our most eloquent attempts fall short of fully conveying the ridiculous, magnificent, miraculous experience of being. Our senses are at the heart of all this wonder. They are the interface between our inner selves and the outside world. They equip us to perceive beauty, from great art to the grandeur of the natural world, and to appreciate a sip of an ice-cold drink, the sound of laughter, the touch of a lover. Senses are, in short, what make life worth living. Our sensory receptors harvest a multitude of textures, pressure waves, patterns of light and concentrations of molecules to feed myriad pulses of electrical information, like an army of hyperactive stenographers, to the brain, which decodes, organises and, ultimately, weaves meaning. This extraction of meaning from the jumble and chaos of physics is what makes us, us.

My own understanding of the senses is forged from the perspective of a biologist and through my studies on the sensory ecology of a variety of different animals at the University of Sydney, and before that at universities in the UK and Canada. My research has examined which stimuli guide the behaviour of creatures, from insects to whales, and thus how each experiences its own domain. The greatest challenge that comes with this is to try and set aside my human-centric biases, to comprehend things from very different perspectives. While I can never perceive things quite as other species do, I can at least attempt to shed the certainties of my sensory experience and endeavour, so far as I can, to see the world through their eyes. It's this process more than anything that ignited my passion to know more about the senses, not only in other animals, but in us.

As a biologist, it's essential to understand why it is that evolution has equipped us with the senses that it has. To do this, I delve into the sensory lives of creatures – from the mammals with whom we share a recent common lineage to those that are far distant from us, such as crustaceans and even bacteria – to learn about the origins of our senses and the ways in which our experience differs from theirs. While this is primarily a book about the human senses, by exploring the sensory worlds of other animals we can gain a deeper appreciation of our own.

In my quest to understand the senses in the broadest possible way, however, I soon realised that I had to reach beyond my own field. The senses are not just about anatomy and physiology, for all that some of the drier textbooks may present them as such. An approach that restricts itself to processes doesn't begin to convey the wonder, or the deeper meaning, of the senses. Freeing myself from the constraints of a purely biological viewpoint, I immersed myself in research from disciplines as diverse as psychology, ecology, medicine, economics and even engineering and I delved into the question of how thoughts, emotions and culture shape, and are shaped by, our sensory world.

My challenge was not only to understand the senses but to place them in the context of our lives and it's the challenge that has inspired me to write this book. While I don't neglect the underlying biology, my goal is to examine our senses in the round. For this reason, I leave the more detailed biochemistry, molecular and cell biology to other, more specialist books. Instead, I examine not only how we sense, but why. I'll delve into the fascinating questions of how we each differ in our sensory experiences and where these differences emerge from. I explore how our senses have shaped humankind and I look to the future, to predict how the senses will influence what is to come.

I've arranged the book by devoting a chapter to each of our five primary senses before turning my attention in Chapter 6 to a host of underappreciated but crucial senses. But while such an approach has the benefit of neatness, it runs the risk of implying that each sense is separate and segregated from the others. This, as I show, is far from the case; all of our senses are interdependent and fascinatingly so. As a result, I examine the many interactions between the different senses throughout the book, and especially in the final chapter, where I explore how our brains weave the miraculous tapestry of perception from a medley of sensory inputs.

When I began this book, I came to it full of enthusiasm for all aspects of our sensational existence. The research that I've done in the intervening years has only amplified my appreciation of this incredible topic. The Nobel laureate, Karl von Frisch, once described the process of learning about a subject for which you nurture a great passion as being like a magic well: the more you draw from it, the more it fills with water. I wish you, the reader, a similarly wonderful experience as you dive into the extraordinary world of our senses.

What the Eye Sees

A view comprehends many things juxtaposed, as co-existent parts of one field of vision. It does so in an instant: as in a flash, one glance, an opening of the eyes, discloses a world of co-present qualities spread out in space, ranged in depth, continuing into indefinite distance.

– 'The Nobility of Sight', H. Jonas

Sight is sometimes regarded as the ultimate arbiter of truth. When we're told of some fantastic episode, we might reply that we need to see it for ourselves. Yet what we see isn't reality, it's a narrative created by the brain. Subconsciously, the brain takes the raw input from our eyes and it freights the raw input with meaning, filtering the observations and subjectively ascribing qualities and biases, filling in gaps as it goes. Most of the time we're unaware of this, investing our recollection of what we've seen with confidence and certainty, as in the phrase 'I saw it with my own eyes!'. This reliance on vision represents a degree of overconfidence since sight is the sense most prone to being tricked. We even try to fool it for ourselves, for instance when we wear 'slimming' colours, or when interior designers resort to tricks of the *trompe l'oeil* variety.

The sham only begins to reveal itself when we experience an illusion. One of the most basic forms of this is known as the Müller-Lyer illusion, where two identical lines can be seen, usually presented parallel to one another. Both are bookended by a pair of V-shapes; one has the Vs arranged so it looks like a double-ended arrow, while the other has them pointing inward. The fact that the Vs stick out further from the latter makes the line seem longer, even when we know that isn't the case. It's a simple example, which exploits the fact that how we see things depends on the visual context in which we see them.

Context isn't everything, however. The autokinetic effect describes how points of light might seem to move as we look at them. The German scientist and philosopher, Alexander von Humboldt, wrote about 'swinging stars' he claimed to see moving in the night sky. You might experience the same illusion of movement if you gaze at a star, particularly on an evening when relatively few others are visible. It's perhaps understandable how some people interpret such apparent celestial agitation as proof positive of visiting alien ships. But the most compelling example of the effect comes from studies where participants are asked to look at a single, stationary point of light on a screen and are told that the light is moving in a certain direction. Primed with this information, the participants most often agree that the light is moving as suggested. Best of all, in another, similar study, experimental subjects were informed that the light would spell out a specific word, although they weren't told what the word was. Of course, the static light couldn't spell out any words; if the participants saw anything, it could come only from their imaginations. Yet when asked, many insisted they had seen a word, and in some cases refused to disclose what the word was because it was rude.

The brain gathers only the gist of what's in our visual field beyond the thing that we're concentrating on. That's why we suffer from phenomena such as inattention blindness, most famously evidenced in a video that went viral on social media some years back. Asked to count the number of passes made between a group of basketball players most people were so caught up in the task that they didn't spot a person in a gorilla suit walking through the frame. We're attuned to the big picture and we're good at recalling the essence of what we see, but very few people have the capacity to recount the details of a given scene, something which makes eyewitness testimony a rather hit and miss affair. We look, but we don't always see. Even with all of these flaws and inconsistencies, we are arguably, more than anything else, a visual species. Oddly, however, it's a sense that we very much have to grow into.

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It is hard to think of a more profound and intense experience than that of being face to face with a loved one, silently contemplating one another. We overwhelmingly look at, or into, the eyes and we're conscious of seeing and being seen. When fathers gaze at their newborns, evolutionary theory tells us that they're looking for something: a resemblance. Across different cultures, nonpaternity rates average a little over 3 per cent. In other words, around one in thirty fathers of newborns aren't the father at all. Perhaps it's for this reason that mothers (who, after all, can be reasonably confident of being the parent) are four times as likely to point out their baby's resemblance to the father than the other way around. A study carried out in 2009 asked people to rate the similarity between fathers and their children and then followed up by asking the mother to give feedback on how good a dad their partner was. The results were remarkable. The greater the resemblance, the more effort the fathers put into raising their children. Overall, the more confident a man is that the child is his, the more he tends to invest in that child, and one of the most important elements in generating that confidence is the similarity that the father perceives in his child's appearance. It has to be said that as I regarded my son on his first day at home, I wasn't aware of making any such assessment. All I knew was that this dribbly, incontinent bundle of gurgles was the most wonderful thing I'd ever seen.

It's perhaps fortunate for my son that at the age of less than a week and with my unlovely face looming over him, his vision wasn't great. Much of what he'd have been able to see would have been a blur. This is common to all newborns; the clarity and definition of whose vision is only around 5 per cent of that of a normally sighted adult. They can see faces, but only at a range of around 30 cm, which handily is about the distance from their mother's breast to her countenance. Faces are arguably the most important things that we, as intensely social animals, have to recognise. The basics of this ability are present even before we're born, particularly the tendency to relate to a rough configuration of two eyes abutting a nose with a mouth below. Third trimester foetuses respond to light patterns shone on their mum's belly and when an arrangement of dots and lines is used in an approximation of a face, this holds their attention for much longer than other, similar constellations.

Our tendency to tune into this most basic of facial contours – essentially two dots and a line – is why we're so prone to seeing faces in clouds or on the fronts of cars. Fortunately for us, our ability to recognise faces is a little more complex than this, but the way that we achieve this sheds some light on why two dots and a line can at least begin to fool us. Recognition is achieved by a network of neurons in the brain. Each group of cells within this network attends to a specific characteristic of a face, and then in collaboration, the groups build a composite picture that we use for identification. Among all of the complexities of a human face, however, it's the crucial pattern of eyes, nose and mouth that anchors our perception and provides a kind of mental canvas onto which we can map the other features.

We, like many other mammals, are born incomplete as sensory animals. Our genes provide a kind of rough draft of the neural equipment needed for perception in our brains. This rough draft is shaped and honed by experience, especially in the critical first weeks and months of our lives. Missing out on this experience can lead to lifelong deficits. Mice reared in the dark never fully establish sight to the extent that those with a more typical rearing environment can. The same is true, sadly, for people who lose their sight as infants and later have it restored through surgery. In visual terms we're born as beta versions, stimulating and reorganising the brain simply by looking around us. It takes around six months to fully hone and train our sight, which is testament to the staggering intricacies of human vision. It was not always this way. Far back in evolutionary history, what we now think of as sight began as merely the ability to register light.

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Of course, we can never know exactly how light detection evolved or what form it took in ancient times, but it seems likely that it wasn't too different to the equipment that some modern single-celled organisms now possess. Photosynthetic bacteria gain their energy from the sun – thanks to light-sensitive proteins they can, at some level, register the presence of light, but the problem for many of them is that they don't know where it's coming from. Consequently, they blunder around their environment until they chance upon their equivalent of a sunny glade. The alga *Euglena* boasts a much greater degree of sophistication. It's just one cell, but it can sense light and it has a whippy little tail known as a flagellum that it uses to propel itself towards it.

Guided by similar light-sensitive pigments, a sapling detects a gap in the forest canopy and hurries up to meet it. If the light strikes the sapling at an angle, part of the plant will be in shade. The cells on the shady side respond to this solar snub by extending and elongating, which has the effect of bending the tip of the plant directly towards the sun. Some fungi, such as *Pilobolus*, take this a step further. *Pilobolus* specialises at growing in the rich, moist environs of animal turds, and like all good parents, they look out for the interests of their offspring. For the next generation of *Pilobolus* to prosper, they have to be eaten as spores by an herbivorous animal and subsequently evacuated along with some ready-made fertiliser. The problem, however, is that grazers tend to avoid feeding too near dung. What the adult fungus must do is find some way of flinging its spores into a different neighbourhood and this is where it's essential for them to be able to detect the sun.

Like our sapling, these so-called hat-throwing funguses can sense light and turn towards it. To assist them, they have an important refinement. At the very top of their slender stem, they have a transparent sac of water. This enclosed globule of liquid acts like a lens, focussing the sunshine onto light-sensitive cells below and allowing the fungus to register the sun's rays more effectively. In the early morning, when the sun's light hits the fungus from the horizon, the fungus bends towards it and does the job it's named for: it throws its 'hat' – in reality, a parcel of spores sat right on top of the fungus's makeshift lens. The water in this lens is at such high pressure that when the sac ruptures, the package of spores is subjected to a G-force twice that of a bullet fired from a rifle. By aiming at the rising sun as it's low in the sky, the fungus ensures that the kids go sideways rather than straight up. So the spores are propelled to a bright new future, well away from the parental pile.

Surprisingly enough, this simple approach to light detection also occurs among animals, many of whom can detect changes in light with their skin. When a shadow passes over a sea urchin, the prickly (but eyeless) little creature realises it might just be about to come under attack and bristles its spines in response, declaring itself up for the fight. Shine a light on the tail of a lamprey, or on the larva of a fruit fly and they scoot off to find shelter – in both cases, a response that's independent of eyes. Pigeon chicks sit up and beg for food when the light above them changes, a cue that they're hard-wired to associate with the arrival of their parent. Amazingly, they do this even when they're wearing a hood that completely covers their head, but they don't do it when they're attired in a cape that blocks the light from their entire body. The responses of all these creatures are achieved with the help of photosensitive proteins in the skin that register the presence of light.

Relatives of these proteins can be found in our own bodies. As we awake each morning and open our eyes, light streams in and sets in motion a cascade of events that ushers away sleepiness and gets us ready to face the day. It does this courtesy of an extraordinary protein, known as melanopsin, which can be found sprinkled around various locations inside our heads and within our eyes. When light hits melanopsin, the protein does a little molecular dance that results in the sending of a message to the suprachiasmatic nucleus deep in the brain. In response, the bundle of nerve cells therein shut off production of melatonin, the hormone responsible for preparing us for sleep, and kick-start our bodies into action. Melanopsin is specifically excited by blue light, which is a feature of the backlit screens that we like to gawp at, and it's one of the reasons why it's a terrible idea to take your phone to bed. Reading such a device activates melanopsin, in turn persuading the brain to keep you awake.

Impressive though melanopsin is, it doesn't enable you to see. Its job is simply to register the presence of light; it's a long way from detecting light to vision, and for this you need eyes. Gliding around on a carpet of ooze at the bottom of a pond, tiny creatures known as flatworms carry the most rudimentary versions of these organs. Towards the front of the flatworm's body is a pair of eyespots, clusters of light-sensitive cells situated within little cup-like depressions. Like many shady characters, the flatworm likes to stay out of the limelight. Armed with its eyespots, and particularly the directional shading provided by the cup, it can tell where light is coming from and can use this to remain in the shadows.

It's perhaps forgivable from a human perspective to feel a little underwhelmed by the mere ability to detect where light's coming from. After all, the flatworm's visual abilities don't seem to represent much of an upgrade on what a fungus can manage. But pause for a moment. Just being able to orient yourself according to a light gradient represented a revolution in the history of life of Earth. For a microorganism like *Euglena*, it means the ability to hog the sunniest places and to merrily photosynthesise while less sophisticated competitors lag in its wake. For a flatworm, it means the ability to find shade. Such creatures have a competitive advantage over those that lack their light-finding nous. Ancient organisms that were equipped in this way were rewarded through natural selection; they have more offspring, which tend to inherit the very qualities that made their parent a winner.

Even so, we're still some way away from eyes. More specifically, the bit we're missing is the precise reason that you can read this page: the ability to form an image. How did we get from mere light-sensitive patches to the glorious sense of vision that we enjoy? Our eyes, and the whole visual processing systems of our brains, are so intricate and comprise so many essential components that it seems incredible that they could arise incrementally. In reality, we can hypothesise how this happened and, crucially, as we retrace the steps of more than 500 million years of ocular evolution, we can see examples of eyes in various stages of complexity in the animals around us.

Starting with the flatworm, the deeper the pit that contains their eyespots, the better the job this pit does of casting a shadow on the light-sensitive cells that reside within. If the opening of that pit is relatively narrow, what you effectively have is something like a pinhole camera. No lens is needed, but the effect is that light entering a narrow aperture will project a simple image on the opposite side. Admittedly, the image isn't fabulously clear, but it is nonetheless an image and animals such as abalone and nautilus rely on this arrangement even now. Building on these foundations, the development of the eye gathers pace. It develops a transparent covering of skin, perhaps originally to keep pathogens out, that evolved in time to become the cornea. The lens, too, developed from skin cells with high concentrations of transparent proteins known as crystallins. The sensitive cells that perform rudimentary light detection in animals like flatworms developed into the exquisite structural array that we know today as the retina. A combination of the lens and the cornea bends light into shape and focusses it onto the retina, allowing us to form a beautifully clear image.

It would be wrong to imply that the evolution of eyes represents some kind of predictable progression of biological achievement from primordial light-detecting bacteria to some pinnacle in modern humans. Many eminent biologists have hazarded guesses at the number of times that vision has independently evolved over the last 500 million years, ranging from a handful to hundreds. Regardless of what the correct number is, it's certainly true that there's a dizzying diversity of eyes in the animal kingdom, some of which are demonstrably superior to ours. And like so many products of evolution, our eye is assembled from a hotchpotch of available components and represents a series of compromises. The genes involved in coding the development of the eye are scattered around our genome rather than being collected together at a single point. What's more, those 'eye' genes have histories that extend way back to a time before eyes existed. The original role of some of these genes was in coding a kind of cellular stress response, comparable to that which causes our bodies to tan following exposure to ultraviolet light. The bottom line is that the genetic equipment needed to build an eye didn't appear out of nowhere, but rather involved taking a bit from over here, another from over there and so on.

The result is an excellent eye, for sure, but it's by no means flawless. The most obvious glitch is our strange back-to-front retina. The blood vessels and nerves that respectively supply the retina and connect it to the brain are on the side that faces toward the outside world. As a result, we have a blind spot where the optic nerve wires straight through the retina. And if blood vessels become clogged, or leak, this can interfere with the passage of light to the retina with the effect that vision is blurred or blocked. Biological engineering often bears these hallmarks of imperfection.

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Imperfect though the eye may be, it's an entrancing organ to behold. If you look closely into someone's eyes, the chances are that you'll notice a beguiling pattern of colours around the iris, but also a tiny reflection of yourself in the deep black of their pupil. It's this that gave the pupils their name, from the Latin *pupilla*, or 'little doll'. Perhaps more than any other part of the body, the pupils are a giveaway to our mood. They dilate when we're aroused and as such, they act to communicate our interest. It's why some poker players elect to wear dark glasses as they play. The response is involuntary – there's not a great deal we can do to mask this and for that reason the pupils are to some extent an honest signal of how we're feeling. Though it's something we're only subconsciously aware of, when we interact with people whose pupils are enlarged, we regard them as warm and friendly, because they appear to be fascinated by us. In past times, women used to exploit this quirk of human nature by dousing their eyes with tincture of deadly nightshade. The effects of doing this are twofold. First, the nightshade blocks the muscles that contract the pupil, which has the effect of making the pupil alluringly large. And second, it blurs vision, and makes it difficult to focus. In consequence, women who adopted this technique would appear to be powerfully attractive right up until they stood up, tripped over the cat and went face first into the chaise longue. Still, the upsides to this rather hard-core treatment were such that the use of it by the ladies of Renaissance Italy was commonplace and their enhanced appearance gave nightshade its alternative name, belladonna, or 'beautiful woman'.

Toxic shortcuts aside, the way your pupils respond when you look at others really does give a tell-tale indication of sexual orientation, although it differs according to your gender. A study that examined the pupils of subjects while they watched raunchy film clips reported that the way they responded correlated with what those subjects described being turned on by. Heterosexual men's pupils dilated more in response to seeing a video of a woman rather than one of a man, while the pattern in gay men was reversed. For women, the picture was more complex. While gay women's pupils reacted more strongly to other women, straight women's pupils responded more or less equally to either sex. This latter pattern has attracted some interesting explanations. Based on conversations I've had with female colleagues, I think it might reflect the greater nuance in female sexuality and female perspectives generally. Rather than suggesting that heterosexual women are secretly bisexual, it may be that while they find the male actor physically attractive, they also empathise and identify with the woman in the video, independently of any sense of being attracted to her. Other explanations are available …

Just like a camera, the eye has to do more than simply let light in, it has to bend it in such a way that it becomes focussed. This job is done with a little teamwork between the cornea and the lens. The cornea sits on the surface of the eye, above the iris and pupil, protecting the delicate structure from damage, while the lens is positioned on the inside of the eye, behind the iris. We're used to thinking of the lens as being the senior partner in this, but around two thirds of the eye's focussing work is done by the cornea, before light even reaches the lens. Nevertheless, it's the lens that's in charge of the fine-tuning.

Two hundred years ago, the scientist Thomas Young was puzzling over the question of how the eye brings objects into focus. One idea was that the eye itself changed shape, in particular getting longer or shorter from front to back to change the distance between the lens and the retina, just as cameras do. But how would you test this? Young did what I'm sure any of us would have done in his position: he stuck metal keys in his eye socket to clamp his eyeball. His thinking was that if he could prevent his eye from changing shape, he'd learn whether it was this that allowed him to focus. But with his eye held captive in this bespoke torture apparatus, he looked around and realised everything was in focus, gaining both greater understanding and a sore eye. Having ruled out shape changes in the eyeball and in the cornea, Young arrived at the correct conclusion, which was that it is the lens that changes shape to allow us to focus.

Despite his impressive commitment to the experiment, Young was frustrated in his attempts to work out just how the lens changes shape. We now know that our flexible lens is pulled into different shapes by surrounding muscles. Contracting these muscles makes the lens transform into an almost round shape, which bends light dramatically and is exactly what's needed when you need to focus on something close up. As you get older, the lens becomes less flexible and the muscles that control it become weaker, making it harder to see nearby things. Until we reach the age of about thirty, we can focus reasonably well on objects that are only 10 cm from our face. This so-called near point then recedes until, by the time we're aged sixty, it's 80 cm away, necessitating either long arms or special glasses. Going the other way, plenty of people of all ages suffer from short-sightedness. Part of what's happening here is that the eyes focus light onto a point in front of the retina rather than directly on it – it's sometimes said that myopia is the result of having elongated eyeballs.

Lining the back of the eye is the endlessly amazing retina, a thin strip of multilayered tissue at the back of the eye that translates incoming light to nervous signals. It's amazing not only because of what it does, but also because of what it is. The retina is neural tissue, so although it's on secondment to the eye, it's still technically your brain. Indeed it's the only part of the brain that can be seen without cutting into the skull. If you removed the retina and flattened it out, it would cover an area of less than a quarter of a credit card yet crammed within that space there may be more than 100 million photosensitive cells, dedicated to the collection and communication of information from light.

It's a little over 100 years since this incredibly complex, multilayered structure was first properly described, by a man whose early life gave no hint to his later greatness. Santiago Ramón y Cajal was born in northern Spain in 1852. His early life was characterised by a rebellious streak, which saw him barred from a series of schools and perennially dodging the local police. To his father's exasperation, Cajal dedicated his energies to fighting with other boys and devising weapons for this purpose. Rather impressively, this culminated in his construction of a homemade cannon, which he used to destroy his neighbour's door and for which the amateur artilleryman spent a few days in jail. He was saved from delinquency by his passion for art, particularly painting and photography, and science, to which he devoted himself outside the strictures of the classrooms that he so detested. You can see the confluence of art and science to wonderful effect in the incredible drawings that he produced of the nervous system, particularly the retina. Most important of all, he discovered that the cells in the retina connected with one another to make an intricate communication network, a kind of biological precursor of the sensors found in a digital camera's scanner, that could collect detailed visual information and relay it to the brain.

The problem for Cajal was that his findings ran contrary to the prevailing scientific viewpoints on the nervous system. This might have represented a problem, were it not for his inexhaustible willpower. Frustrated by the lack of recognition accorded to his work, he travelled to Berlin, then the epicentre of world science, on a mission. Once there, Cajal didn't so much introduce himself to Albert von Kölliker, the most prominent scientist in his field, as drag him to look at his new findings. Whatever the propriety of this, it worked. Von Kölliker became his most enthusiastic supporter, and Cajal's work laid the foundations for our understanding not only of the retina, but of neuroscience more generally.

Cajal's exquisite diagrams of the retina show not only its many layers, but the two critical types of cells that detect light. These cells are named for their basic shape: rods and cones. Each contributes to vision in a different way. Rod cells don't allow us to perceive colour, they give us a sense of light and dark in monochrome – a kind of fifty shades of grey. Nonetheless, they're more sensitive to light than cones, so are particularly useful in low-light situations. By contrast, cone cells are sensitive to specific wavelengths of light and so give us our perception of colour. The way this works is quite ingenious. Humans typically have three different types of cone cell, each of which specialises in a different wavelength of light: short, medium or long, which roughly translates to blue, green and red. All of the colours that we see are produced by mixtures of these three colours. This is the basis of what's known as the trichromatic theory, an idea that was anticipated by our eyeball-squeezing friend, Thomas Young. It's also why each pixel on the screen of your TV, or your iPhone, has three little dots of colour within it, allowing the screen to mix these in various ways to produce the full range of colours. It's not possible to see these in the screen under normal conditions, but put a tiny drop of water on the screen and look again. The magnifying effect of the water droplet lets you see the pixels and their colours.

As schoolchildren, we're told about the primary colours – red, yellow and blue – those that can't be made by mixing other colours. Strictly, red, yellow and blue are the subtractive primary colours.* Sunlight and the lights we tend to have in our homes are a mix of all possible colours, which is to say they're white. When white light hits something, such as the pigments in paint, or the petal of a flower, certain colours are absorbed – subtracting them

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* It's actually more correct to say that cyan, magenta and yellow are the subtractive primary colours. That's why printer cartridges bear these names. The colour red is made by mixing magenta and yellow, while blue is a blend of cyan and magenta.

from the mix – while others are reflected and this reflected light is what we see. So when you see a ripe tomato, for instance, its redness emerges because the fruit absorbs all the colours except red, which it reflects. And when an object absorbs all the colours, then that object appears black. But this subtractive scheme only applies when light bounces off objects, like tomatoes, on its way to our eyes. When light comes direct to our eyes from its source, however, things change and we need a different set of primary colours, referred to as the additive primary colours. Coloured lights, such as those you see on a screen, are additive. You start with no light – darkness, in other words – and add colours. You get white light by mixing the three additive primary colours: blue, green and red. Working out how other colours are generated in the additive scheme can be perplexing, largely because those art lessons in early life remain prominent in our minds. For instance, we know that to make orange paint, we mix red and yellow together. By contrast, orange light is a mix of two parts red to one part green.

Our own experience of colour emerges from the way that our brains interpret detailed information coming in from our cone cells. While each type of cone cell is a specialist in a particular colour, each is also responsive to adjacent colours on the spectrum. For instance, our green cone cells don't only get stimulated by green light, they'll register shorter wavelengths like blue, and longer ones towards the red side of the spectrum. The crucial thing is that they only get really excited by green, pinging an enthusiastic message to the brain when confronted by a lettuce leaf, for instance. When they detect a colour either side of green on the spectrum, their passion is dialled down. The same is true for our other cones, and since the range of colours to which each reacts tends to overlap to some degree, the brain can triangulate the information coming in from the three cones to calculate the colour. When we're confronted by something yellow, for instance, our red and green cones fizz with enthusiasm, while our blue cones languish like teenagers at a golden wedding celebration. When encountering a turquoise object, the red cones have little to say, but the blue and green cones are piqued. In each case, the brain interprets the input from the different cone types to provide us respectively with the sensation of yellowness, or turquoise-ness.

Right at the heart of the retina lies an area known as the fovea, from the Latin for 'small pit'. Despite its miniscule dimensions – it's less than half a millimetre across – cone cells are crammed into this little depression in our retina. Not only that, but each of the cone cells here has its own direct connection to the optic nerve, the information superhighway to the brain, and the result of all this is that the fovea provides our greatest visual acuity. This acuity, effectively our ability to distinguish detail, is what's measured by your optician. If you have normal vision, sometimes called 20/20 vision, you'd be expected to be able to read a letter that's about 9 mm high at a distance of 6 m.

Unusually, in terms of acuity as well as motion sensitivity, men tend to outperform women. It's a strange aspect of the human senses that sex differences exist, and in all of our other primary senses as well as in some other features of vision, women have the upper hand. Why would acuity and motion sensing be different? Perhaps it's because millions of years of living as hunter-gatherers placed a premium on the ability of men, who are thought to have done the majority of the hunting, to discriminate detail at long distance and to detect movement of prey animals. The truth is, we don't know. Nevertheless, the differences are small and both men and women have excellent acuity compared to many other mammals. For instance, cats' vision hovers around the limit to be declared legally blind for humans. Dogs do slightly better but still have far lower acuity than us. By contrast, birds of prey have incredible acuity, often well over twice as sharp as our vision, and possibly up to four or five times better, allowing them to see rodents and small animals scurrying around on the ground far below as they soar.

But our impressive visual acuity refers mostly to that which our fovea provides. Outside that area our acuity falls away, which is why your peripheral vision is much less sharp. Retinal cells outside the fovea are less densely packed and have to share their connection to the optic nerve with their neighbours, so the information coming from them is less clear. Rods, which primarily support our peripheral vision, are excellent at detecting the changes in our visual field that indicate motion, but don't supply much detail. When we detect something moving in our peripheral vision, we don't get a clear sense of what it is. An early warning is good in the sense that we can leap out of the way, but it's also the reason we might reflexively apologise to a post box for walking into it.

It's a facet of our sensory systems that when we detect something interesting around us, we present the most sensitive receptors towards it. So when we see something out of the corner of our eye, we reflexively turn to fix that object on the fovea. The vanishingly small size of the fovea means that even viewing something from a distance of 2 m, the area that we see with greatest clarity is only about 4 cm across. Imagine you're looking at someone's face when you're talking to them. Your fovea is sufficient only to see their mouth, or one of their eyes, in high definition. Our visual system has a trick up its sleeve to deal with this: every second, the eye makes dozens of infinitesimal movements, scanning multiple regions of the person's face, which your brain knits together to make the view appear seamless.

If you imagine the retina as a dartboard, the fovea represents the bullseye. The further you go towards the margins of the board, the density of cone cells decreases and their place is taken by rods. Whether your eyes are relying primarily on sharp, full-colour, cone-based vision or the less detailed, black and white perspective provided by the rods depends on how much light there is. As night sets in, there's insufficient light to activate the cones and the rods start to take over. As this transition takes place, the peak sensitivity of our vision shifts away from red along the colour spectrum towards blue. An enjoyable way to experience this for yourself is to enjoy an evening drink in a beer garden and watch how the colours change as it gets darker. The reds fade first, well before greens and blues. If you have the patience to remain, you might be rewarded with a view of the stars scattered across the night sky. Since there's little light, we see them thanks to our rods, which makes them appear white. It's strange to realise that most stars aren't white at all, but a panoply of different colours. To see the full technicolour glory of the stars, you need to amplify the amount of light that reaches your eye from them, which means a telescope. Doing this means that your cone cells kick into action and provide an appreciation of the rainbow of colours above your head. Contrary to our familiar colour coding for temperatures, the hottest stars are blue, or bluey-white, because of the high-energy, short wavelengths of radiation they emit. Cooler stars such as Betelgeuse are reddish in colour.

Throughout our lives, we're bathed in energy that radiates from the stars, including our own sun. We can arrange the different forms of radiation along a spectrum – the electromagnetic spectrum – according to the energy it produces. The Earth's atmosphere screens most of this from reaching us, but crucially two types of radiation do make it through. Low-energy radio waves are one type, which is why we use radio telescopes to study distant galaxies. The other type we call light.

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The electromagnetic spectrum encompasses a vast range of energies and amid these, there's a vanishingly small segment of radiation, something like 0.0035 per cent of the spectrum, that we can see and which we sometimes refer to as the optical window. Our atmosphere is transparent to these wavelengths and, happily for us, they pass straight through. But in the context of the evolution of vision, these wavelengths were confronted by another