

Animal senses: how do they perceive the world and what important things can they sense that we cannot? Professor Keith Kendrick

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Introduction

In the next three lectures I will consider how we and other species experience the world around us and in particular how, as social beings, we and they recognise each other and have a capacity for self-awareness. All this, of course, requires at the outset some appreciation of how the senses work and how they differ between species.

An important starting point in considering the way we and other species sense the world is the simple statement that whatever sense is being used it is merely providing an interpretation of the outside world. In short we do not sense the world as it is but merely as our sense organs interpret it within the limitations of their design. One might even say that our senses provide us with the comforting illusion of experiencing an absolute reality that is, in effect, only relative and highly subjective. This illusion makes it difficult for any individual to appreciate the fact that the same world can, and does, appear very different to other species and indeed even to other individuals of one's own species.

From an evolutionary standpoint of course any species develops only the specific senses, ranges of detection and levels of sensitivity that are required for its members to interact successfully with the environment and survive. Only humans have taken the step of developing sophisticated artificial sensors to detect chemical molecules, light particles, sound waves and electromagnetic energy beyond our own biological sensory capacities. The amusing fact however is that for all our amazing inventiveness in many cases other species have evolved equivalent, or even superior, biological abilities to sense cues from the environment that are only available to us with the aid of machines.

We have come to accept the existence of five primary senses in most species. These are divided into those which require some aspect of the environment to achieve physical contact with the individual (touch and taste) and those which detect remotely either at close range or at variable distances (smell, hearing and sight).

Our experiences through the different senses are effectively our point of contact with the outside world and allow our sense of individuality with respect to it. It therefore comes as no great surprise that sensory deprivation is one of the most effective human-devised tortures. Cut off from its sensory input the brain simply loses control.

We are all well aware that different species have different capacities to use these five primary senses and we will examine some of these in detail in a moment. Most of us are also aware of claims that other senses may exist that allow detection of objects by echolocation (or biosonar as it is now called) and electric fields, direction guidance using sun compasses, celestial maps and detection of electromagnetic fields. Finally,



and most controversially, are the claims of being able to sense telepathic signals at distances beyond those where other senses can be utilised. Indeed, as far as the telepathic sense is concerned it is often claimed to be prevalent in species who have continued to stay close to the natural world but has been lost in humans whose progressive detachment from things natural has rendered this ability vestigial.

Even a casual look at special sensory abilities that have been claimed for other animal species is pretty impressive:

 \cdot Dogs and cats who know the moment their owners form an intention to return home (even if hundreds of thousands of miles away in some cases).

 \cdot Dogs detecting previously undiagnosed illnesses such as cancer or being able to give their owners warning of an impending epileptic attack or high blood pressure.

· Animals being able to detect hormonal changes in other animals or humans.

 \cdot Animals being able to sense emotional states in humans or other animals either in their presence or even when physically separate from them.

· Dogs being able to detect the presence of humans even when they are buried.

· Dogs and cats being able to trace their owners and making long journeys to be re-united with them.

 \cdot An impressive range of species being able to find their way back to a particular place from a distant and totally unfamiliar location.

 \cdot Animals being able to detect electromagnetic fields, infrared and ultraviolet, use sun compasses and read celestial maps.

- · Animals having the ability to locate objects and individuals by sonar.
- · Animals able to sense impending storms, earthquakes etc.

There are, of course, many more such claims. As we will see, many of these phenomena can easily be explained by understanding the different sensory abilities of other species.

However, before examining in more detail the different ways that animals experience the world in comparison with us, and whether there are in fact more than five senses, it will be useful to illustrate the general principles upon which the primary senses function. This will hopefully provide a useful guide to understanding both the nature of individual sensory experiences and the defining criteria required for establishing additional sensory modalities.

General principles of sensory systems

Whatever sensory system one considers the most important first component to identify is the receptor device that converts, by transduction, the relevant external signals from the environment into electrical impulses that can be conveyed to, and interpreted by, the brain. To date we know of five basic types:

(1) Chemoreceptors - which are activated by the shapes of specific chemicals through receptors on their cell membranes (i.e. smell and taste receptors)

(2) Mechanoreceptors – which are activated by forces displacing physical sensors, such as hairs, attached to the cell membrane (touch and hearing receptors).

- (3) Thermoreceptors in the skin which sense temperature
- (4) Nociceptors in the skin which sense pain
- (5) Photoreceptors which are activated through surface receptors and absorb light (visual receptors).



There are also likely to be magnetoreceptors for detecting magnetic fields although it is still unclear as to what, or even where, these receptors might be (I will return to this question later).

All these receptors are located external to the brain and the electrical signals they produce, when activated by the relevant external stimuli, are conveyed to the brain by bundles of nerves. Sensory acuity is mainly associated with the number of receptors dedicated to sensing a particular aspect of a sensory stimulus – i.e. a specific wavelength of sound or light, the sensitivity of any particular body region to touch or the ability to detect the taste or smell of a particular chemical. It has less to do with how sensitive specific sensory receptors are since they are usually able to respond to the minimum unit of an energy source - one or two particles of light, decibels or chemical molecules. However, in many cases receptors vary in the duration of their response to a particular stimulus with some adapting very quickly and others more slowly. This adaptation is important since one of the main uses of our senses is to detect changes in the different energy sources around us (whether in location, intensity or type) and so invariant exposure to the same energy source will result in the receptors initially detecting but gradually adapting to it by adjusting their thresholds upwards. Indeed this makes our sensory systems less than optimal for performing repetitive tasks (bulk wine or food tasting or quality control of mass produced identical objects). This is why robotic sensors can offer advantages since this adaptation component can be omitted.

In general the organisation of the neural projections from the sensory receptors through the sensory nerves to the brain faithfully maintain the same spatial representation as the pattern of sensory receptor activation. This means that the initial spatial and temporal pattern of activation within the brain regions receiving the information picked up by the sensory receptors is reproduced so that the brain can start off its interpretation of the sensory cues using the same physical map as the receptors themselves. To further complicate matters some senses (particularly vision) have multiple maps dedicated to the extraction and analysis of the different components of information conveyed by the receptors.

Of course, not all things are of equal importance as far as sensory detection is concerned. The general principle is therefore that where a particular sensory modality, part of the body, light or sound wavelength, or chemical molecule is of greatest importance for some aspect of survival then not only will more receptors be employed for detection but also correspondingly more of the brain. So even if you knew relatively little about the preferred habitat and behaviour of any particular animal species, you could deduce much simply from knowing what kinds and numbers of sensory receptors they have evolved and the amount of brain dedicated to analysing the information received from them.

One conceptual problem that arises is that the initial representative maps of the different sensory modalities within the brain are all physically separate – that is as far as the brain is concerned our immediate experiences of the sight, sound, smell, taste and feel of any particular object are independent of one another. Even though sensory information from these specific sensory processing regions does eventually become integrated, particularly in those areas involved with controlling some form of behavioural action, we are likely to be aware of what the different senses are detecting before this happens. Thus we have the vaguely schizophrenic conclusion that, to a large extent, the brain can allow us to be independently aware of our experience of the world through each of the different senses.

While we are left with the uncomfortable general conclusion that our brains through the different senses are capable of simultaneously experiencing multiple independent illusory interpretations of reality it is clear that the separatist principles that have evolved when dealing with multiple senses are there to avoid confusion (a point I will return to later on when I consider synaesthesia).

Let us now examine how these principles work with some specific senses.



The sense of touch

The skin is our largest sensory system and if unfolded has an approximate area of 50 square feet. It has different receptors for heat, cold, pain, itching and pressure and this is the case in mammals in general. If we just concentrate on the pressure sensitive receptors, which effectively represent the sense of touch, and how these send projections via spinal nerves to somatosensory maps (somatotopic maps) within the brain, then we can see immediately how both we and other animals have vastly different touch sensitivity from different body regions.

In humans, the surgeon Wilder Penfield was the first to map the human somatosensory and motor cortices. What he found was firstly that the most sensitive body regions were disproportionately represented. Thus, more of the brain is devoted to touch stimuli from the genitals, lips, tongue hands, face and feet than the whole of the rest of the body. Indeed, as far as the brain is concerned our body representation of touch sensitivity is a very strange looking homunculus with these regions disproportionately enlarged!

A second point of interest is the way the different body regions are juxtaposed in terms of their representation in the brain cortex. In humans the somatosensory cortex is a narrow band extending the whole width of the cortex with the left and right sides of the body being represented respectively in the right and left hemispheres of the brain. If we move along this cortical band from the most lateral point of the brain towards the middle of it the batting order is throat, tongue, jaw, lips, face, nose, eyes, thumb, index, middle, ring and little fingers, hand, arm, shoulder, head, body trunk, hip, leg, foot, toes and genitals. For the most part, whatever species one considers there is a similar kind of juxtaposition of body-parts although the shape of the somatotopic map is often more like a huge blob on the cortical surface of the brain in highly tactile-dependent species rather than a narrow band.

An important principle is that this touch map within the brain is very much use-dependent and it has been shown in monkeys that preferential use of specific fingers can double their cortical representation. One shudders to think what generations of hand-held computer-game devotees may have done to the cortical representations of their thumbs!

From the other side of this scenario there is the question of what happens when limbs are amputated. Here juxtaposition is an important consideration since the body parts represented adjacent to the missing part tend to invade its space within the cortex. This can result in bizarre phantom limb experiences – for example individuals with a missing hand may report an apparent sensation in it when part of the face is touched. In another instance an individual missing the lower half of his left leg reported his experience of sexual orgasm as extending to include this phantom limb. Indeed, since there is a least some overlap between the brain representations of different body regions it has been argued that foot fetishes are particularly prevalent since the feet are represented immediately adjacent to the genitals!

The increased importance of touch in mammals that rely more on this sense than vision and hearing (particularly those that are mainly nocturnal or live underground) is illustrated by the large amount of brain dedicated to processing touch information relative to areas dealing with sight and sound. It is also reflected in the huge numbers of receptors, and associated brain processing, in their noses and whiskers which are the areas of most importance for navigating their world and locating other individuals and food. A primary example of this is the famous star nosed mole that has 100,000 touch receptors in its nose and over half of its entire somatosensory cortex dedicated to them (indeed this represents around 20% of the entire brain cortex!). To put this in a human context this represents six times the maximum touch sensitivity of the human hand.

Similarly nocturnal animals such as the raccoon mainly use their hands to locate food and other individuals and also have high receptor numbers and disproportionate representation of their hands within the brain.

Animals with such enhanced sense of touch in specific body regions are likely to have a corresponding enhanced sensitivity to pain in them since nociceptor numbers should also be increased. They are also likely to able to detect low-level earth vibrations and subtle alterations in the environment that we would be unable to detect. This could, for example, help them to identify the start of earthquakes and storms well before we would be able to.

Smell and taste

These two chemical senses do clearly work in conjunction with one another since the experience of flavor is a combination of activation of taste and smell receptors (and indeed touch sensations on the tongue) although the sensitivity of those responding to odorants is much higher than those responding to tasteants. This explains why having a bad cold can dramatically impair one's experience of food flavors and why you can't taste the difference between a potato and an apple with your nose plugged!

The sense of taste

As far as the sensation of taste is concerned there are five or possibly six different receptor types and the exact experience is determined by the respective pattern of activation that occurs across these different receptors. Broadly speaking all of these receptors are distributed in the tongue (and indeed other mouth areas – epiglottis and soft palate) although there is some enhanced regional sensitivity to specific tastes (most text books illustrate distinct spatial locations for the different receptors but they are not correct – indeed no area of the tongue is sensitive to less than four different taste qualities). The receptors detect salty, sweet (sugars), sour (acids), bitter (alkaloids) and umami (glutamate receptors, i.e. detects monosodium glutamate and meat-like tastes). Recent research suggests that there may be fat receptors as well. These receptors are aggregated in groups of 30-100 in taste-buds embedded in the surface of the tongue with access to the chemicals on the tongue via pores.

The sense of taste both promotes appetite for safe foods and immediate rejection of toxic ones. Life being what it is, the system is biased towards detecting potential poisons so receptor detection thresholds are better for sour and bitter tastes (which suggest potential poisons) than for salty and sweet ones!

Taste information is relayed via several cranial nerves to the brainstem and then to the somatosensory cortex adjacent to the region dealing with the sense of touch in the tongue. At this time there is no reported meaningful topographical representation of the different tastes in this region although it is likely to turn out that there is one.

As with the sense of touch, experience can increase the number of taste receptors so food and wine tasters can enhance this sense. Similarly, other animals can presumably adapt to local conditions by varying the representation of their taste receptors, although less is known about how other animal species have adapted their taste systems in comparison with ours. However, many other mammals have greater total numbers of taste buds than us (rabbit – 17,000; pig – 15,000; human – 9000) suggesting they may actually have superior taste sensitivities!

Interestingly, there are also large general variations in taste receptor numbers with about 25% of individuals (mostly female) having around 1100 taste buds/cm2 (who readily detect bitter substances and often consider sweet food has too much sugar and are rarely overweight), 50% with around 500 and incredibly 25% with fewer than 100 (mostly men – in this case individuals like bitter foods such as coffee and cheddar and eat more salt and sugar than on average and therefore are more likely to be overweight). It has been proposed that enhanced taste sensitivities in females may be used to protect them from ingesting toxic foods during pregnancy. Indeed, the period of morning sickness in pregnant women

corresponds to the most vulnerable period that embryos have during development (when the internal organs are being generated and the foetus is very sensitive to damage by even low levels of toxins) and represents the result of increased sensitivity and aversion to foods that are particularly likely to contain some toxins (vegetables and meats). Miscarriages are actually less likely to occur in women who experience severe morning sickness.

The sense of smell

This is the sense where the popular view is that most animals are superior to us. This view is largely correct with some dogs being claimed to have 1000-fold better detection levels for odours than us. Indeed, many breeds can identify individuals or food even when enclosed or buried or perhaps 100 metres or more away (provided the wind is in the right direction).

To complicate matters, smell detection is carried out by two different sets of detectors and brain pathways that have probably evolved separately. This is because the chemicals that compose particular odours are either air borne or in liquid form (i.e. urine, saliva or glandular secretions – often referred to as pheromones).

Both systems are remarkable in having huge numbers of specific chemical receptors, 100 or so for liquidborne odours and 1000 or so for air borne ones. The air-borne odour system can use these to detect an incredible 10,000 or more different smells.

Detection of pheromones

This is an ancient sense which is likely to mainly evoke involuntary behavioural or hormonal changes in response to specific smells.

The receptors are located in a small organ located in between the roof of the mouth and the nose (Jacobson's organ or the vomeronasal organ). They send their projections via a nerve to a small specialised processing region in the brain (accessory olfactory bulb) and then onwards to parts of the limbic system controlling emotion and the hypothalamus controlling sex and the release of hormones into the blood. Thus the right smell evokes an immediate and unconscious emotional, sexual or hormonal reaction. The stuff of dreams as far as the perfume industry is concerned!

For some species of mammals such as hamsters and pigs, the male sexual response depends on female pheromones activating this system. In mice it is used by females to recognise the male that has mated with them. If the female is then exposed to a strange male his novel pheromones will cause her to abort her pregnancy.

For some time it was thought that humans did not possess this ancient form of chemical detection but it now appears that it does exist and many of the receptors have now been identified. However, despite repeated attempts to demonstrate that this detection system can unconsciously provoke sexual or other emotional or endocrine reactions in humans no clear evidence has been provided. This has not stopped it being referred to as the potential 6th sense and the subject of intense speculation.

Detection of air-borne odours

For detection of air borne odours the 1000 different types of receptors are located in the olfactory epithelium of the nose. The huge increase in olfactory sensitivity seen in some other mammals compared to us is reflected in the area of the olfactory epithelium and the numbers of receptors involved. Thus the

dog has 150 cm2 of epithelium, the cat 14 cm2 and humans only 4 cm2.

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These receptors send projections via the olfactory nerve to a primitive region in the front of the brain, the olfactory bulb. Here the nerves from the same type of receptor converge giving this brain region a form of spatial map where each different chemical odour activates a separate region. This map can however vary with intensity which may help explain why the same odour can be perceived differently at different intensities. Most biological odours are made up of a number of different chemical components and so their representation ends up as a complex pattern of all the different individual elements. This representation of complex odours can also be increased as a result of learning.

After the olfactory bulb signals are processed by a small cortical structure, the piriform cortex which still maintains some of the spatial information patterns. From there it is sent to parts of the limbic brain dealing with emotion (amygdala) and memory (hippocampus). It then reaches the frontal region of the neocortex which integrates it with other senses and is also important for aspects of memory and controlling attention and behavioural action as well as linking into brain centres mediating reward.

The organisation of this sensory system, like the pheromonal one, is thus relatively simple compared with hearing and sight but it does involve areas of the brain that allow it to be a sense that we, and probably other species, can be conscious of. The other important aspects associated with it are that its direct links into brain regions controlling both memory and emotion, make it both a highly memorable sense and one where recognition almost invariably evokes an immediate emotional reaction (whether pleasure or disgust).

The survival value of this sense is therefore obvious in that it provides a highly sensitive means of detecting, remembering and locating things that can make you feel good or bad with the minimal amount of thought and even when there is not much light!

Although the larger numbers of odourant receptors in many other mammalian species, by comparison with humans, allow them to detect concentrations at levels where objects can be detected at great distances down-wind, a major use of this sense is more proximal – i.e. nose down, following trails left on the ground or for detecting buried food.

The human sense of smell should still not be underrated and since the way our brains are organised to detect odours is very similar to that of other mammals we can, to some extent, use our own experience to consider what it must be like for a dog with a threshold 1000-fold lower than our own. For us smell is also a highly emotive sense. As Rudyard Kipling put it:

"Smell are surer than sights or sounds to make our heartstrings crack"

The whole field of aromatherapy is also centred around this concept with large numbers of smells being claimed to influence our general alertness, stress and mood:

Chamomile: calming and soothing. Eases anger and anxiety Clary sage: relaxing, euphoric. Eases anxiety, tension and stress Eucalyptus: fresh cooling and invigorating. Promotes alertness Jasmine: alleviates anxiety and depression Lavender: calming. Helps relieve pain. Lemon: refreshing and energizing. Eases tension. Heightens mental clarity Mandarin: relaxing and calming. Relieves insomnia Neroli/Orange blossom: relieves stress, anxiety and insomnia

Peppermint: refreshing and stimulating. Increases alertness. Relieves pain, indigestion, nausea and headaches.

Rosemary: a stimulant that promotes mental clarity and alertness.

Sandalwood: warm, sensual aroma. Euphoric and seductive.

Ylang-ylang: alleviates anger, anxiety and stress

(Hammers, 1995)

Like us, and in line with the principles of all sensory systems, the receptors will adapt to constant exposure to particular odours by becoming less sensitive to them and so there is not a constant experience of information overload. However, when new smells are present they will probably be experienced with the intensity of a physical blow and an immediate feeling of pleasurable attraction, fear or disgust. Thus, when a dog is following the odour trail left by a rabbit , another dog or its owner it is probably constantly being encouraged to continue doing this through a strong experience of pleasure and excitement.

For the majority of humans we are only infrequently aware of changing smells in our environment but for animals like dogs it seems likely that life is made up of a constant experience of detected changes in smells.

Our body chemistry is altered by what we eat, or by whether our immune system is trying to fight off disease, by hormonal changes and by different emotional states. This is then reflected in altered chemical compositions of our excretions (saliva, sweat, urine, faeces) which can be detected by those animals with a super-sensitive sense of smell (notably dogs). From an evolutionary standpoint this is a very useful advantage to have in deciding who to reproduce with, whether to fight with or escape from an individual, whether another animal is dead or not and if meat is good to eat or not. Doctors used to use their sense of smell to aid diagnosis in their patients before it became simpler to send of blood or urine samples for analysis of chemical changes. However, a number of labs around the world are working on perfecting artificial nose technologies to aid in rapid, non-invasive diagnosis of human disease. Death, of course, also results in a dramatic biochemical changes which animals with a keen sense of smell could detect.

Hearing and biosonar

In mammals hearing different sounds across a range of different intensities is initially the result of pressure waves entering the ears and vibrating the large surface area of the ear drum (tympanic membrane). This in turn vibrates the three small middle ear bones (malleus, incus and stapes) at the same frequency which transmits and amplifies them via the oval window (15-30 times smaller than the ear drum) into the cochlear of the inner ear. Here the waves mechanically activate hair receptors embedded in the basilar membrane through the vibrations setting up a shearing force along it in conjunction with the tectorial membrane. Different frequencies are detected by the hair cells along the length of the basilar membrane. This membrane varies in width and thickness so that different frequencies effectively vibrate the hair cells in different portions of it. Sound intensity is signalled by altered wave amplitudes more strongly (high amplitude) or weakly (low amplitude) activating the receptors. The highest frequency sound waves resonate the part of the membrane nearest the oval window (where it is thickest) and the lowest frequencies resonate the portion furthest from the oval window where it is widest and thinnest.

The greater hearing sensitivities of many other mammals (notably dogs and cats) compared to us is once again mainly the result if having more peripheral receptors dedicated to the task. Indeed, turning up the gain in this way also means that such animals are going to be detecting changes in the sound environment almost constantly rather than just periodically. It also means that loud noises are more likely to be avoided since the levels of vibration they cause in the ear membranes and receptors will actually cause pain.



The bones of the middle ear are held in place by small muscles, which, if contracted, will stiffen the structure, and reduce hearing sensitivity. We, and other animals, do this when we vocalise, making it harder to hear anything else when we speak (Don't speak when I'm speaking to you!). For this reason we actually hear the noises we make ourselves mainly through the bones of the skull and these can directly vibrate the final ear bone, the stapes. This is why when we hear recordings of our own voice (detected mainly through the ears and all three ear bones) they sound different from the way we sound when we hear ourselves speak. In marine mammals such as the dolphin the ear has become vestigial and sounds, whether self produced or externally derived, are actually detected through vibrations set up in the lower jaw being transmitted into the cochlear via the stapes.

As with the other sensory systems the spatial arrangements of the different frequencies in the receptors of the cochlear are faithfully maintained in the auditory nerve projections into the brain. Thus different portions of the auditory cortex contain cells tuned to different frequencies and larger regions are dedicated to processing the most common frequencies. There are also associated maps responding to frequencies detected by both ears (binaural).

Direction of sound is computed using the time difference for it reaching the two ears and the shadowing effect of the head reducing the intensity of sound reaching the ear screened by it. Ideally, detecting phase differences in sounds arriving at the ears requires the size of the sound waves to be twice the distance between the ears. For a mouse this equates to 12-20Khz whereas for humans it is 1Khz. Thus animals with small heads are bound to be more sensitive to higher frequencies than us.

As with the other senses, experience can have dramatic effects on the cortical representation of different frequencies so you can become better attuned to hear sounds that have particular importance.

The two main differences between our own sense of hearing and that of some other mammals lie both in its sensitivity and the different frequencies that can be detected. Thus large land mammals such as elephants can detect infrasound frequencies as low as only a few Hz whereas we can only go as low as 20-40Hz. Indeed, elephants communicating with each other use low pitched sounds that are very hard for us to detect and allow them to hear other animals calls 8 or more kilometres away!. On the other hand many other mammals are capable of detecting ultrasonic frequencies well beyond our maximum range of 20kHz. This includes most rodents (mice up to 100KHz), dogs (up to 45KHz), cats (up to 64KHz), bats (up to 120KHz) and dolphins (up to 100KHz).

Advantages of infrasound

Low frequency sounds penetrate virtually everything and as such are transmitted incredible distances. Whales, elephants, giraffes, lions, hippos and rhinos all communicate with one another using this frequency range (which is mostly inaudible to us). For this reason they can communicate with each other over huge distances. So at least in some species this explains their ability to locate and communicate with each other at what seem to be impossible distances. This low sound frequency is transmitted well through the ground and elephants can apparently detect other elephants stamping the ground in fear 50 kilometers away. It has been calculated that elephants may routinely be able to be identify these sounds over an area of 100 square kilometres. With cetaceans they have the added advantage that sound travels four times faster in water than air and this may explain their ability to locate each others calls even when hundreds of kilometres apart.

Even the smallest earth tremors (low frequency seismic waves) preceding earthquakes should be detectable by animals with good hearing in the infrasound range. Similarly low-frequency noise transmitted from distant thunderstorms or rain falling on the ground would give considerable notice of imminent weather changes in the area where the animal is.



As humans we appreciate the advantages of stealth technology for being able to approach enemies undetected. Another evolutionary advantage of both infrasound and ultrasound capabilities is to mask communication from the ears of other species that you may want to catch or stop from catching you.

Advantages of ultrasound

High frequency sounds are better for short-range communication since they are easily reflected by objects and localised. Large numbers of mammals use ultrasound frequencies to communicate and in many cases (apart from echolocation) to indicate some form of distress (babies calling to their mothers or adults in pain). One exception to this is in male rodents where they emit ultrasonic vocalisations after having sex with a female. Clearly this is not pain although whether it is a sign to the female to back off until he is ready to have sex again or the consequence of physical exertion is open to speculation!

It seems likely that predatory species such as members of the dog and cat families have evolved ultrasound detection abilities to help detect the presence of prey species since they do not seem to use these frequencies to communicate with one another.

Biosonar

The evolution and use of biosonar (echolocation) in animals is a remarkable story and its complexity makes it impossible to go into detail here. Many consider biosonar to be a distinct additional sense although I prefer to see it as a specialised adaptation that utilises the sense of hearing. The superstars of biosonar are insect catching bats (Microchiroptera) and dolphins, although the fact that these species use biosonar differently and lack common evolutionary ancestry suggests that they have evolved this ability independently.

Most is known about echolocation in bats. These animals live together in caves in vast numbers (often many millions) and come out at night to hunt insects. They can use echolocation to detect even the smallest moving insects at distances of 3-4 metres and can catch 300-600 of them every hour. They can do this in absolute darkness and don't seem to need their eyes at all. This is high speed hunting carried out at 20-30 mph and from detection to capture takes less than 0.5 seconds.

They do this by emitting frequent, brief ultrasound calls which have a constant fundamental frequency of 30KHz with three integer harmonics at 60, 90 and 120KHz. When an insect is detected there also a downward-sweep frequency modulated component at the end of the call. The intensity of the 60KHz component is the loudest and so this is the most important for detection. Indeed, the intensity of this is so loud that it has been equated to the level of sound we might expect to experience at a Rock concert. Amazing to think that several million bats could be flying around making more noise than one could almost possibly imagine but as far as we are concerned they appear to be mute!

The bat's calls are focussed by structures on the head and are perfectly designed to bounce back from even the smallest of objects. The flies are moving in relation to the bat and so the echoes bouncing back from the calls are subject to a Doppler effect which shifts their frequencies upwards. The bats compute the differences in time and sound intensity of the echo arriving in the two ears to determine directional changes. Differences in the magnitude of the Doppler shift are used to calculate distance. Greater localisation accuracy is also achieved by systematically increasing the frequency of calls as the bat closes in on the fly

Their auditory cortex has a linear map of the different frequencies in the bats auditory range but large amounts of cells are dedicated to precise detection of 30, 60 and 90KHz. The problem with this is that Doppler-shifted echoes might differ from this by as much as 0.5KHz and the system would not detect them very well. So in addition to increasing the frequency of its calls as it catches up with the fly the bat systematically alters the pitch of its call so that the Doppler-shifted returning echo is always at 30,60 and 90KHz (this requires remarkable vocal control that would be the envy of any opera singer!).

The wing-beats of insects affect the patterning of the returning echoes and the bats are even sensitive enough to such minute changes to allow then to determine what sort of fly it is they are chasing. After all, we all have diet preferences and bats would not want to be disadvantaged by not knowing what exactly was going to be in their next mouthful!

One other major problem is that with several million competing bats firing off calls all around you how can each individual know which echoes belong to its calls? The solution is truly simple, but still remarkable. In the first place echoes from ultrasonic calls can only be detected over 3-4 metres so that limits the number of possible competing sounds from other animals. Just like us, when the bat vocalises it contracts the muscles on the bones of the middle ear and therefore cannot hear the low intensity 30KHz signature frequency of other bats. Like us it hears this frequency from its call through the skull linking to the stapes bone and not through its ears. It will also sound different and have a highly personalised specific frequency which will differ from the other 30KHz sounds perceived by the ears. In its auditory cortex it has another map of auditory frequencies where cells only respond if a 30KHz frequency is either followed by a 60 or 90KHz one with a particular time-difference. Since the bat can't hear the 30KHz component of any other bat when it makes its call, and can tune these brain cells to register only to the precise frequency with which it hears its own voice, then it can be sure its call has started the activation sequence. Having located its prey it also has a pretty good idea when a 60 or 90KHz echo should be received and so the cells guiding the animal will only be those which are activated by a subsequent 60 or 90 KHz echo arriving at the right time. In this way it is unlikely that the animals will be confused by the calls and echoes from dozens of other bats flying near them

Dolphins probably differ only in that they use broader band calls (or clicks as they are often called) which are effective over longer distances (they can detect a 5cm ball at 120 metres). They also differ in that they produce the clicks through the nose rather than the larynx and hear the echoes through their lower jaw linked to the stapes bone (the dolphin's ear opening seems to be largely vestigial). They also focus their ultrasound using a structure called the melon in their nose and have adapted amazing ways of using fat encasing their hearing apparatus to prevent problems of impedance matching when sound transmitted through water moves into air in the middle ear.

Thus, the different hearing ranges experienced by other species, or the use of biosonar, can give them information from the world that we can appreciate only through machines. In particular they can allow long-distance communication and localisation of even the smallest objects in complete darkness. Once again they may also aid detection of environmental changes well before our own senses can.

Vision and magnetoreception

The visual sense is of course the one that we are most reliant on and where, to a large extent, we have considerable advantages in terms of acuity and ability to interact with the environment in daylight compared with other mammals. It is also the most complex sense and I will only describe it in a fairly superficial way (see Zeki, 1993 for more detail) and concentrate on differences between us and other mammals. Light entering the eyes is focussed onto the retina by a lens. The retina has two types of light-sensitive receptors: rods (which are sensitive to low levels of light at all frequencies), and cones (which are sensitive to light at specific frequencies).

The fact that the visual sense can interpret the world through so few receptors compared with some other senses is perhaps surprising but it has the important consequence that the brain does much more interpreting work than with the other senses. This conclusion is easily demonstrated by the host of visual illusions that can be shown to trick or confuse the system. The eye also focuses the world upside-down on the retina but, the brain turns it back the right-way up. Finally, even though we have blind spots where our optic nerves leave the eye to take visual information into the brain, the brain fills in the gaps for us so that we are not aware of this gap in our visual world.

All animals have some form of central area of highest sensitivity in the centre of the retina and the eyes are directed to bring important objects into the central field of vision which allows the light from their image to fall on the densely packed receptors in this region.

Humans, other primates and many predators have eyes that are mainly located facing forwards in the head which improves the degree of binocular overlap and visual acuity in a limited field of view. Primates also have developed the most sophisticated control in being better able to move the eyes independently of the head so that light from the salient features of any particular scene or object can be more quickly brought into the most accurate field of view. On the other hand most prey species have more laterally placed eyes which, in many cases, can almost give a full 360 degree range of vision although a more limited field of binocular overlap. Thus the field of view experienced by a rabbit or sheep is much wider than for us or monkeys.

Most other mammals are better adapted to a nocturnal existence than ourselves and have more rod receptors in the retina and many have a structure called the tapetum in the eye which reflects captured light back onto the retina for a second time to further enhance sensitivity. In such animals this makes their eyes shine brightly in the dark when exposed to light.

Humans and other primates perceive colours by having cone receptors which are sensitive to light of three different wavelengths, red, green and blue (trichromatic vision). However, a number of mammals only have two such receptors (dichromatic). Dichromatic vision is considered to have advantages for the detection of movement (which is clearly important for most animals) and while trichromatic vision is not as good in this respect it may have evolved to allow primates to improve visual resolution and to distinguish between different coloured fruits and leaves more easily.

The way that the brain processes the visual signals reaching it from the eyes is remarkably complex and has been the subject of huge amounts of research. However, the general principle is the same as other senses in that the spatial pattern of light influencing the receptors in the eye is reproduced in the primary visual cortex. This performs a first-pass analysis of light intensity and direction and then sends this on to other regions that are specialised for analysing motion, colour and shape and even some regions where specific objects, such as faces, are encoded (an area I will cover in my next lecture). The connections between this primary visual area and all the others is mainly parallel in nature with the same region of cortex connecting with multiple other regions. Thus visual experience is mainly the result of different aspects of the visual stimulus being assessed by physically separate parts of the brain simultaneously, and this gives rise to an integrated and synthesised perception. For this reason damage to different parts of the system can result in highly specific deficits such as the ability to see colours, movement and shapes although other aspects of visual cues are still experienced.

There is little doubt that other animals experience the visual world somewhat differently to ourselves. Many have considerably less cone receptors and nerve projections to the brain which downgrade both visual acuity and the vividness of color perception (for example the dog optic nerve has 167,000 nerve fibres compared to 1.2 million in a human). On the other hand many mammals (cats, dogs and sheep for example) have up to six times better visual sensitivity than us in the dark since they have many more rod receptors. These latter receptors are probably also responsible for giving these species greater sensitivity



to visual movement than us.

If we express daylight visual acuity in other animals as a percentage in relation to humans, horses and sheep have 50-60%, dogs have 40% and cats have 20% of our acuity. Put another way the acuity of a cat viewing an object placed 20 feet away would be the same as that for a human viewing it from 100 feet away (i.e. a cat has 20:100 vision compared with human 20:20 vision).

In contrast to us many other mammals only have cones sensitive to two (dichromatic) rather than three (trichromatic) wavelengths. This greatly reduces the numbers of colours than can be seen (similar to humans with colour blindness due to the lack of a particular cone receptor). For the most part it is the long-wavelength cone (red) that is not represented giving the animals similar experience to humans who are red-green colour blind. As trichromats we can distinguish four basic hues (red, blue, green and yellow) which can be seen as a continuum of hues through proportional mixing. For dichromatic animals (and red-green colour blind humans) only two hues can be distinguished (blue and yellow) and rather than mixing intermediate hues are either achromatic (white or gray) or a desaturated version of one of the two basic hues (i.e. pastel blue or yellow). Thus the world is likely to appear slightly blurred with a predominance of pastel yellows, greens, blues and greys (Carroll et al., 2001).

Of course humans are not the most sophisticated species for either visual acuity or colour. Some birds (especially birds of prey) and insects have more types and numbers of photoreceptors giving them a much more sophisticated colour sense and greatly enhanced acuity.

Some animals (notably some birds, ants, bees and some fish) have also developed photoreceptors that are sensitive to extremely short wavelengths in the UV range. This allows these species to calculate the position of the sun by detecting patterns of polarised light at different times of day (allowing compass navigation using the sun even when the sun is not actually visible – see Hughes, 1999). It also allows some birds of prey to detect small rodents whose urine trails have a UV content. At the other end of the spectrum some snakes have receptors that can detect longer wavelengths in the infrared region of the spectrum which allows them to detect the heat generated by potential prey. Mammals however do not seem to have adapted to detect either UV or infrared frequencies.

Magnetoreception

It is now well established that many migratory species of birds and fish have sophisticated abilities to detect the earth's magnetic fields to allow them to find their way across hundreds or even thousands of miles without having to rely on either the position of the sun or the stars (see Hughes, 1999). Indeed all these species are unable to perform this feat if they have magnets attached to them that prevent them from detecting the weak magnetic fields of the earth.

For many years the nature of the magnetoreceptor has been the subject of considerable debate and the main stumbling block to accepting this as a bona fide sense. Much of the initial focus has been on the possibility that we have biological magnets in our heads capable of transducing magnetic fields into electrical activity to be processed by the brain. This initially received support from the demonstration that such a material, magnetite, was indeed present in simple organisms such as some bacteria and allowed them to orientate north (in the northern hemisphere) or south (in the southern hemisphere) in response to magnetic fields. Bees also appear to have such magnetic receptors linked in with their nervous systems. Elegant studies in trout have also now established similar connectivity between magnetite-based receptors and the brain via a branch of the trigeminal nerve. Most mammals, including humans have such magnets in their heads, particularly in the nasal area but to date no connectivity with the brain has been established although mammalian brains, including our own, do show altered activity in response to magnetic stimulation.

A number of recent proposals have suggested that magnetic fields may actually be detected through their known influences on photoreceptors in the retina (Ritz et al., 2002). This idea has received recent support from a study in the mole rat showing that a primitive visual area in the brain, the superior colliculusis strongly activated by magnetic fields with the direction of the magnetic fields being represented in different layers (i.e. another potential example of a map)(Nemec et al., 2001). This makes a lot of sense because this brain structure is important for controlling the way we immediately change our orientation (i.e. turn towards or away from) in response to both visual and touch cues. This same system could obviously do the same thing for responding to magnetic fields.

In humans one study has concluded that many of us can tell which is North and South without the aid of visual directional cues although we are apparently better at it if we are either naked or wear cotton than if we wear synthetic static-producing substances like nylon. We are also better at it apparently if we normally sleep in a North/South orientation (Baker, 1995).

There is little doubt that many mammals are better able to detect changes in magnetic fields than ourselves. This ability may not only give directional guidance but also advance warning of electric strorm. Electrical activity in our bodies also sets up local magnetic fields and so it is conceivable that just as we can used magnetic resonance imaging to view activity in our brains, other species may have the ability to detect changes in our physiological or emotional states by detecting changes in the magnetic fields we, or other animals, produce.

It is likely that the sensing of magnetic fields is a very primitive biological system, rather like the pheromonal one, and involves brain regions that do not promote significant awareness. In this case it may be more like either travelling unconsciously down a homing beam where alarms are only raised when there is a mismatch between intended and actual directions, or feeling comfortable, or not, through being in the presence of another individual.

Are our experiences of the different sensory modalities always separate?

Imagine what it would be like if music was not just heard but could also be seen in terms of colours and felt in different parts of your body, or alternatively if specific words always triggered a simultaneous sense of a particular flavor or colour. Life might be seen as a rich and complex experience but would also be more than a little confusing and an exhausting state of sensory overload at times.

This condition can indeed happen in humans and has been called "synaesthesia" (literally syn = together + aesthesis = perception) and was first reported by Francis Galton in 1880. Most recent reports suggest that it occurs in between 1 in 200 and 1 in 20,000 individuals, depending upon how strict a definition is used. In its most common form individuals see specific graphemes (numbers or letters) as coloured (even though they are not) although which colour is seen varies from individual to individual. However, the 5 senses allow for up to 20 different varieties of synaesthesia involving two senses and most of these have been reported. The main examples are sounds evoking visual experiences of colours although some bizarre combinations have been reported such as a man who experiences tastes as shapes and a woman who experiences different musical instruments as tactile experiences in different parts of her body (see Cytowic, 1993).

One thing that is most common is that visual experience is evoked by one or more of the other senses rather than the other way around.

Not suprisingly this condition has often been associated with artistic individuals – Vladimir Nabokov, Olivier

Messiaen, David Hockney, Alexander Scriabin for example. A recent report has even suggested that 23% of 358 fine-arts students surveyed reported experiencing synaesthesia.

It is clear that synaesthesia is likely to result from a number of different causes and at a number of different levels in the brain (both perceptual – low-level synaesthesia and cognitive – high level synaesthesia – Ramachandran and Hubbard 2001). Although it is difficult to provide definitive principles for what is going on, the most likely explanation is that in most cases there is cross-wiring between adjacent areas dealing with analysis of different sensory information. Thus our sensory maps within the brain may occasionally overlap.

Simon Baron-Cohen at the University of Cambridge has hypothesised that intermixing of the senses is actually normal in human babies in the first year of life and this is supported by brain imaging studies which show broad overlapping patterns of activity with different sensory stimuli. In both humans and other animals there is a physical pruning of brain connections during early development that reduces interactions between sensory areas of the brain.

While one can understand from the reported experiences of individuals with synaesthesia that this can lead to confusion as well as creativity, it remains an intriguing possibility that for some animal species their experiences of the world might be more likely to be routinely multisensory than our own. This might especially apply to nocturnal animals that appear to have almost redundant visual senses and enhanced senses of smell and hearing. In this case it might be useful for specific smells or sounds to be reinforced through the experience of a corresponding visual sensation. This might actually help to improve discriminatory performance without providing confusion with information being detected by the eyes. The idea is, of course, pure speculation but has some support from humans where recent studies on the blind have shown that when they read Braille by touch this can activate areas of the visual cortex!

Is there a telepathic sense?

I deliberately left this to the end so that it could be shown that a number of observations about animals being able to detect earthquakes, storms, emotions and disease, communicate with one another over long distances and find their way home could be shown to be explained easily though their superior abilities to detect specific different forms of known and measurable energy.

While we still have a large amount to learn about detection of electromagnetic energy produced by humans or other animals one would still be hard pushed to consider that this will explain all of the claims that have been made for special abilities in animals and some humans.

The catalog of often quite rigorously controlled observations provided by Rupert Sheldrake in his book "Dogs that know when their owners come home" for dogs, cats, horses and a number of other species is persuasive and hard to explain at present by detection of energy forms that we accept and for which there are known biological receptors.

In humans we also have a number of documented cases of remote viewing where individuals show themselves capable of describing pictures or other items sealed in containers in a remote location. A famous example is the artist Ingo Swann.

Many would like to believe in the existence of extrasensory perception and postulate the existence of other forms of communication via psychic energy which we may, with practice, be able to detect and which other animals may consider second nature. However, without being able to measure the energy or define how



we are able to detect it physically, all observations will remain phenomenological. Of course our understanding of many currently accepted biological sensory capacities started out in exactly the same position.

Since we still have not established the full potential of sensory systems we do at least partly understand it would seem more politic to concentrate our efforts on completely understanding the capabilities of these.

General conclusions

What we can conclude is that at this stage the different sensory capacities of other species can explain many of their apparent supernatural abilities such as communicating over incredible distances, finding their way to distant places, locating small objects even in the dark, detecting buried objects, human or animal diseases or hormonal or emotional changes and detecting environmental changes such as storms and earthquakes long before we can. It is also clear that not everything that has been claimed either other animals or humans are capable of (communication intentions over very long distances or use of remote vision for example) can currently be explained by what we know of the sensory systems that are known and accepted.

What is also clear is that the different sensory equipment, detection sensitivities and ranges make the experience that other species have of the world rather different from our own. The same world can, and does, seem very different to a dog compared with a human. Equally, it can be experienced in a very different way by some humans compared with others.

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