“Getting to know you”: how do animals recognise each other and us? Transcript

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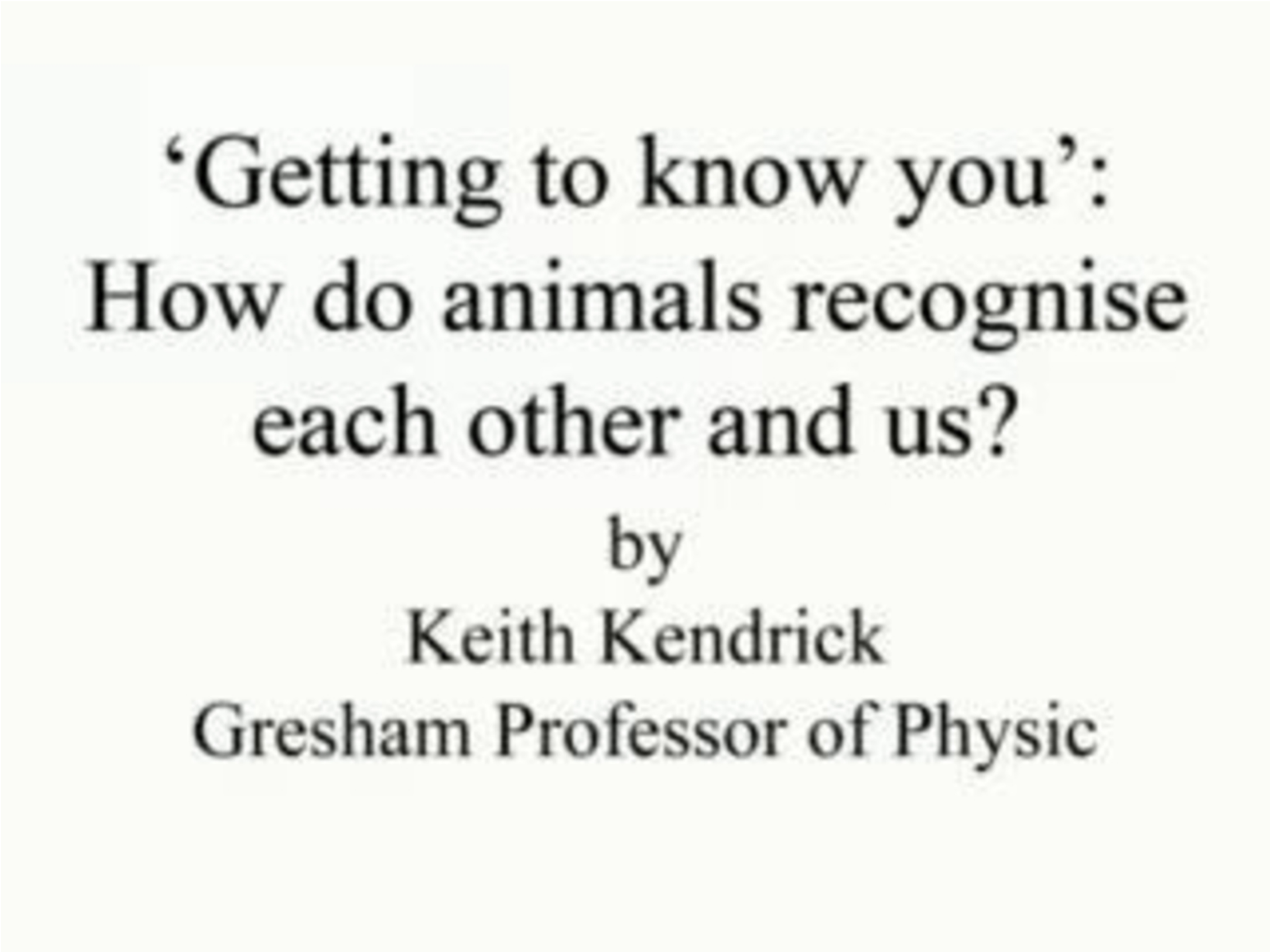

"Getting to know you":

How do animals recognise each other and us?

Professor Keith Kendrick

Having discussed the different sensory abilities of other animal species in comparison to us it is now time to consider how the senses are used to allow social recognition. In this lecture I am going to focus on the three major sensory systems that animals use for carrying out this important task, namely smell, hearing and sight. I will concentrate on giving detailed examples of a few animal species that have been studied extensively and can provide useful exemplars for considering others where less research has been carried out.

From my last lecture it should be clear that the sensory systems of animals have amazing detection and discrimination capabilities and therefore in theory recognising different individuals should not present much of a problem. However, it is the most difficult thing to do for all the senses for a very obvious reason. Your main requirement is to distinguish between different members of your own species but genetically you are all extremely similar and this homogeneity means that successful discrimination is likely to have to take into account a number of different cues and their configural patterns. In short discriminating between individuals of your own species is probably the most difficult thing you use your senses for since other classes of objects that are important to distinguish between have nothing like the same degree of homogeneity.

Social recognition is not just about detection ability but includes the additional requirements of being able to focus attention quickly on the configurations of the most salient cues that distinguish individuals as well as being able to remember them for long periods. To be expert in doing this an animal needs to dedicate considerable amounts of brain processing to recognition memory and the more individuals there are that need to be recognised the more is required. Thus, evolving large-scale individual recognition abilities has a high cost in terms of brain development and processing and any particular species will only develop the skill-level that is optimal for its survival.

Social recognition can take place on a number of different levels? In the first place it may not be necessary to recognise specific individuals at all. Indeed, you can get quite along way by simply being able to recognise your own species and to tell males and females apart. You can add further levels of sophistication to this type of category recognition by being able to recognise any member of a group that is closely related to you (i.e. family - kin recognition) or simply whether they are familiar or not. Similarly you can recognise members of other species that may either assist you in some way or alternatively represent a threat to your life! In short you can achieve considerable survival advantages without having to develop the ability to recognise large numbers of specific individuals.

The main evolutionary drivers for different species to start developing individual recognition skills take us back once again to the main purpose of life, namely reproduction. So if you want to be choosy about who you have sex with, or which babies to dedicate your quality-time parenting skills to, it pays to be able to identify them! Of course, even here, sophisticated individual recognition skills are not an absolute requirement if all that matters is that you can identify any potential sexual partner or have so many babies that it is easier to know generically which ones are yours (i.e. recognising a category rather than an individual). Even where a specific mate or baby needs to be recognised this can be achieved without developing very sophisticated individual recognition skills. A bat can find its baby in a colony of several million or a penguin can find its partner in a group of many thousands. This may not be as remarkable as it seems at first sight. Here it is only necessary to locate one individual with a specific set of signature cues and ignore everyone else that does not have this signature (i.e. in this case individual recognition is only an extreme example of categorisation where a single individual represents the category).

However, social evolution in mammals with its requirement for identifying the different individuals in a social group uniquely has led to brains developing the capacity for remembering a large number of them. In species, like humans and some non-human primates, elephants and dolphins, that live in fission-fusion societies (i.e. where social groups meet up and then disperse again on a regular basis) the numbers of individuals needing to be remembered start becoming significantly large (possibly several hundred or more) as does the requirement for being able to remember them even if they are absent for months or even years.

To establish real individual recognition abilities and their limits it is essential to provide three pieces of evidence:

(1) An animal species must be shown to recognise and respond uniquely to a number of different members in its social group (i.e. not simply restricted to an identifiable category).
(2) The species must be shown to be able to learn to recognise new individuals quickly and remember them even after periods of absence
(3) The specific sensory cues being used for recognition must be identified. Confirmation must be provided that there is sufficient variability in these signals between individuals, and appropriate detection and discrimination abilities in the animals receiving them.

If one can establish true individual recognition skills in any particular animal species this opens up three important additional possibilities:

(1) If you have developed the necessary cognitive skills to identify others as individuals, this allows for the possibility that you can also develop concept of yourself as an individual. This is the essential first step on the road to self-awareness and of awareness of the effects of your actions on others and of theirs on you.
(2) Having the ability to recognise and remember specific individuals is also a step along the path of being able to imagine them in their absence, and possibly even to experience emotional consequences of such imagining (i.e. to miss an absent friend and actively search for them).
(3) One major hypothesis regarding the evolution of intelligence is that it was driven to a large extent by an increased requirement for social interactions and cohesion. The presence of advanced individual recognition skills should therefore be found in social animals and be associated with superior intellect.

As we will see, the path towards establishing true individual recognition in another species can be quite tortuous and has required enormous dedication by researchers. We will start by considering the sense that many other animals have developed superior abilities to us, namely smell.

Individual recognition by smell

In my last lecture I explained how the sense of smell is not only extremely wide-ranging (10,000 different odours detectable) and acute in mammals (particularly in dogs), but also highly emotive and memorable. One might therefore anticipate that discrimination of odour characteristics would be a highly effective method for recognising individuals. Mammalian species that have been investigated in some detail are mice, sheep and pigs and also dogs to some extent.

Can mice recognise each other using smell?
Mice, like humans, can use smell to recognise related individuals with the same immune complex (major histocompatibility complex) and this allows them to show a preference for mating with individuals that have a different MHC complex. This provides an important means of avoiding inbreeding. Are mice also capable of recognising and remembering specific individuals? The answer to this is clearly yes although just how many individuals can be remembered has not yet been fully established

A simple behavioural test to prove their abilities is called the habituation-dishabituation test. Here a mouse is simply exposed to another mouse for 1-2 minutes on a number of different occasions. Recognition is evidenced by a progressive habituation (reduction) in the amount of time spent investigating the stimulus mouse. The possibility that this is simply boredom rather than individual recognition is addressed by introducing a new stimulus mouse at the end of the habituation trials. If the amount of time spent investigating this new mouse returns to the high level seen when the first mouse was encountered for the first time, then boredom is not involved.

Of course this is not terribly impressive if only one mouse can be remembered or it does not last. Evidence so far shows that at least 3 or more mice can be remembered simultaneously after these relatively brief experiences. However, experiments by Harold Eichenbaum in the USA using non-social odours have indicated that they can distinguish between at least 12 of these simultaneously and so they can probably distinguish between a similar number of individual mice. Even more impressive is that the mice can remember the odours of another mouse they have only been in contact with for 2 minutes for 5-7 days.

Curiously, while rats show the same general recognition abilities they will only remember each rat they encounter for a short time (about an hour) although with longer exposure they have also been shown to be able to distinguish between 12 different rats purely by smell. Even in mice durability of recognition following a short exposure period appears to be dependent on your current social conditions since only mice living in a social group remember social odours for a long time. Mice kept in cages on their own become like rats and can only remember the odours of another mouse for an hour or so, if at all. So there may either be a practice effect here or, more likely, a situation where being social reinforces the motivation to want to recognise and remember new individuals.

We know that recognition in these tests is purely based on smell because the animals have no problem with doing them in the dark but can't do so if they are unable to smell. Recognition also occurs even when the stimulus animal is anaesthetised and so could not emit vocalisations towards, or touch, the test animal.

In themselves these tests do not provide absolute proof of individual recognition since the animals could simply be finding common denominators that identify mice that they know as opposed to ones that they do not. To guarantee individual recognition it is necessary to use a test where a mouse is trained so that choice of different individual familiar mice odours is associated with a specific outcome (for example getting food or not). To the best of my knowledge this has not been tested systematically in mice although in has been confirmed in rats.

What smell characteristic is it that the mouse is actually using to recognise other individual mice? The answer to this is that a mouse's signature lies in its urine. Mouse urine is packed full of proteins (major urinary proteins or MUPs) which bind volatile odours and then slowly release them over long periods. The prevalence of urine marking in these and many other mammals allows for such marks to be discernable, and even reconstituted by water when dried out, for long periods. Animals countermark the same urine patch left by others and observers can tell the temporal sequence of who marked the spot when! Mice have 7-12 classes of these MUP proteins that can combine in different patterns - giving a vast number of different potential patterns with which to identify specific individuals. In addition the genes that make up an animals MHC complex also provide specific odour signatures and mice can distinguish between individuals that differ only in a single gene in this complex. The basis for discrimination can even be seen in the area of the brain that processes smell, the olfactory bulb. Here different urine odours evoke different spatial patterns of activation that can be seen even in individuals that only have a single gene difference in their MHC complex.

A study just presented this week at meeting of the American Association for the Advancement of Science (Science 299:1133) has also found evidence for the pheromones from a female mouse's specific sexual partner, as opposed to other males, selectively activating cells in the accessory olfactory bulb of the olfactory system.

Smell recognition in other species
Sheep and pigs have been shown in formal behavioural choice tests to be able to distinguish between individuals on the basis of the smell of secretions from a number of different skin glands. Similarly dogs can distinguish between different humans by the smells on their T-shirts and can track individuals from the smells they leave on the ground. Interestingly, while dogs have difficulty in distinguishing between the odours of identical twins they can do this on the basis of T-shirts they have been wearing for a few days. Thus, while the quality of individual odour characteristics is determined genetically, additional experience-dependent differences can contribute as well.

Of course simply being able to distinguish between the odours produced by different individuals does not in itself prove that any animal actually uses smell normally to recognise individuals. Indeed, we shall see later that for sheep visual cues may normally play a more prominent role even though they have the capacity to use smell.

Another good example of where individual recognition by smell does occur is identification of offspring by their mothers. Sheep mothers, similar to goats, cows, horses and humans, learn to recognise the odour characteristics of their offspring within one or two hours of giving birth to them. Over the following days or weeks they can also learn to recognise their voices and their faces but initially recognition is entirely dependent on smell.

Ability to recognise your own lambs is important for sheep not simply because it helps the mother to find them but also because it makes sure that they do not give out their valuable milk supply to unrelated strangers. So once the mother sheep has learned what her own lamb smells like, any other lamb she encounters with a different smell gets a full measure of her aggressive arsenal of head butts and protest bleats. As I showed in my previous lecture, not only are smells easily memorised by the brain (which is why the mothers of most species, and probably humans as well, learn to recognise their offspring first using this sense), they also evoke almost involuntary emotional reactions. In the case of the sheep the right smell (that's my boy or girl!) evokes the full spectrum of maternal emotional responses, the wrong smell promotes serious aggression. If sheep are unable to smell they will mother any lamb that comes along even though they can distinguish their lambs from others by their voices or faces. The strong link between smell and emotion can obviously have some important advantages for helping mother sheep promote their own genes!

But do mother sheep recognise each of their lambs as individuals? The answer to this appears to be yes. The first piece of evidence that supports this conclusion is that if one twin or triplet lamb is removed from a mother before she has had time to memorise their smell then she will subsequently reject them if they are introduced to her at a later time. This is not due to the smell of the mother's milk since rejection will occur even if the absent lamb is fed with milk only from their real mother. Formal behavioural choice experiments have also indicated that mother sheep are capable of discriminating between the odours of each of their lambs to gain access to food.

Learning to recognise the smell of offspring is actually intrinsically linked with the process of giving birth. Signals from labor contractions directly influence brain structures processing smell information to facilitate their recognition. When we discovered this some ten years ago we were able to find a cheap and effective remedy for the age-old farmer's problem of how to foster orphan or triplet lambs onto mothers that had already bonded with their own ones. The previous main practice for doing this was to physically restrain the mother for 3-5 days so she could not be aggressive towards the orphan and she would, in most cases, eventually accept the lamb. The welfare and economic disadvantages of such an approach are obvious. Instead, we found that for up to 48h after birth it was possible to get 80% of mothers to accept an orphan lamb immediately simply by giving them a manual stimulation of their vagina and cervix for 2 minutes (similar to a veterinary examination). The procedure simply mimics the process of giving birth, just as if the animal had given delayed birth to a second or third lamb of its own. It only promotes formation of a new smell-based recognition bond so the mother does not end up forgetting and rejecting her own lambs.

Of course a similar, although obviously less intense, form of vaginal stimulation occurs during sex. Indeed, in many rodent species (particularly monogamous ones such as prairie voles) recognition of a partner's odour is promoted by sex. Since this mainly occurs in monogamous species it does not really qualify for an individual recognition system that allows identification of many different animals. Indeed, the same process for identifying young does not seem to extend to more than three or four individuals at a time. This is probably what is at the route of claims that many animals don't seem to be able to count up to more than 3 or 4!

Animals recognising humans by smell
We are all aware of the abilities of bloodhounds to track individual humans by smell and there is little doubt that

companion animals in general recognise the specific smells of their owners. This is however after considerable experience with human smells. It is possible that over the thousands of years of humans and dogs living in close proximity, dogs have evolved the ability to be nearly as good at detecting human scents as they are their own. By contrast other species for whom regular human contact is unusual, recognition is mainly generic (i.e. that's a human). Indeed, one can go as far as to say that just as we find many animal species a little bit on the pungent side, they can find our smells pretty disagreeable too. If you get a sheep to smell your hand it may well snort and back-off in just the same way that a mother sheep will find the smell of a newborn goat kid mildly aversive even if it can be induced to act as a mother towards it. This makes sound evolutionary sense because a good way to avoid useless attempts at cross-species matings is to make sure that you find the odours of other species aversive! It also means that you develop your smell sense for discriminating between the different patterns if chemical odours produced by individuals of your own species. The patterns that are relevant for your own species may not work at all well for distinguishing between individuals of another species.

Does perfume aid recognition?
While the individual characteristic smell of any particular animal is genetically determined your diet, hormonal state, immune status and level of arousal or stress can all add to this. To what extent can these other variables influence the important task of identifying the smell of a particular individual? In the film "The scent of a woman" Al Pacino plays a blind man who gives highly evocative consideration to the individuality of a woman's smell. It is not made completely clear whether this is body odour, perfume or both although the indication is that it is probably the latter. The perfume industry emphasises the identity aspect of individual perfumes almost as much as their potential generic attraction to the opposite sex. Is this actually true of other animals, or even for humans for that matter? The answer as far as providing additional cues to identity is concerned would appear that such claims may be false, at least if one considers other animals with a superior sense of smell to out own.

In mice we have shown that adding additional odours to their skin (we use simple non toxic food additives such as lemon and peppermint rather than inflict human perfumes on them or run the risk of being sued for reporting that mice don't appreciate a particular leading brand!) does not normally help at all. Indeed, it would appear that such additional smells are completely ignored in this context. So if a mouse meets another mouse that smells of lemon and meets that mouse again on another occasion it will show the same reduction in interest in it that it would if it had not been wearing the perfume. If it meets the same mouse that had been wearing "Lemon Number 5" on a second occasion but who has now had a TV makeover and is wearing "Essence du Peppermint" instead, it still shows the same level of boredom that would have occurred without the makeover. In short, biological odours are all that are focussed on for individual recognition; the most expensive and exclusive perfume in the world will not change this. The only situation where this is not the case is if a mouse is genetically altered so that it can no longer focus in on the biological odours. This has been achieved through targeted deletion of the oxytocin gene. In these animals they cannot remember whom they have smelled before using biological odours but have no trouble in doing this if they are given a helping hand by perfuming the rear of the mouse they meet up with (Ferguson et al., 2000).

Similarly in mother sheep it was hypothesised that one way of getting them to accept any lamb would be to put a perfume on their own lamb so that they would remember it and then put the same perfume on a strange lamb and they should accept it. Absolute disaster, it does not work at all! So it would seem that biological odours are treated differently from others. Indeed, my own work on sheep has shown that when mothers learn the smell of their lamb there is a dramatic change in the early processing region for smell in the brain with nearly 60% of the cells communicating with the rest of the brain suddenly becoming most responsive to lamb odours compared with other smells. There are also associated changes in neurotransmitter release with own lamb odours evoking large global changes in the excitatory transmitter glutamate (Kendrick et al., 1992). It is unlikely that other odours would provoke a change of anything like this magnitude.

The moral of the story for humans may be that for those considering promoting a deception with an individual by wearing the perfume of their regular partner, the most important question to ask is whether the intended victim is a "man" or a "mouse". If a "man" then perhaps their poor sense of smell might lead them to focus on the perfume rather than the body odour, if a mouse then discovery of the deception will be immediate! The only exception to this would be if we were considering a case of identical twins since the precise biological signature of body odour is genetically determined!

What are the limitations of recognising individuals by smell?
The obvious one is you are at the mercy of the wind and if conditions are not favourable individual recognition by smell can be limited to a range of less than 50 cm. A second problem is that the system, while highly memorable, is strongly linked to brain systems regulating emotion and as such is designed primarily for remembering individuals that have a specific emotional salience. It is not a system designed for recognising and remembering hundreds of different individuals who might be classified as casual acquaintances since they would all have a similar neutral emotional significance. In short, recognising individuals by smell is a system designed optimally for making strong links between identifying a select few that have a distinct emotional importance in your everyday life, it is not for remembering as individuals everyone you meet at a party or a football match!

A final downer for smell dependency is that we have shown in my own laboratory individual recognition memory in mice is very sensitive to hormonal changes. So although females are generally better than males when they have high oestrogen levels at the time of ovulation, at other times during the cycle, and at some stages of pregnancy and lactation, they are not good at all.

Individual recognition by voice

It is now increasingly clear that vocal recognition plays an important role in social recognition in most primate species and for humans it is clearly considerably more effective than identification using the sense of smell. We, and many other animals, also have sufficient variability in the patterns of our voices to allow individual recognition, at least with practice. However, for humans vocal signals are normally most important for communication and identifying important classes of individual (male vs female – pitch, and regional information – accents) than they are for being able to both recognise and remember many different individuals. Committing someone's voice to memory generally requires you hear it quite frequently. To a large extent this is probably also true of most other animals, especially those that have good visual systems. For many other species it may also be mainly a communication medium and a rapid way of distinguishing categories of individual rather than for being able to identify and remember large numbers of individuals outside an immediate small familiar social group.

It is clear however that some species have quite remarkable specialist abilities for individual recognition via differences in voice sounds. These species are mainly those where familiar individuals can be separated by large distances, but where voices can still be used to communicate over them. The two major examples of this are elephants, through their use of infrasound calls, and the calls of cetaceans like dolphins and whales where the increased speed of sound in water and use of infrasound can allow vocal communication ranges of hundreds of square kilometres in some cases.

The call of the elephant
From my last lecture I emphasised the amazing ability of these animals to detect each other's calls over 100 square kilometres or more by using infrasound frequencies (15-24Hz). Sound spectrograms have revealed that the call of each animal is distinct in the same way that human voices are. An extensive series of studies carried out in Kenya by Karen McComb and her colleagues has established that female elephants may be able to recognise 100 or more different individuals and in some cases even remember them for 12 years. The way that this is done is to use what are called "play-back" experiments. In brief this requires the researchers to record the calls of a number of different elephants and observe the behaviour of each animal they are subsequently played to. There is often a major focus on mothers being able to distinguish the various offspring they have produced during the course of their lives. Rather like the mouse smell experiments described above this mainly relies on the fact that elephants will behave differently when they hear an unfamiliar call than a familiar one and the intensity of their interest in the area of the source of the played back call can be proportionate to the degree of familiarity. When a voice is familiar an elephant will approach the source of the sound and sniff the air with its trunk, if it is unfamiliar it promotes a defensive bunching reaction with other members of the herd.

Interestingly discriminatory abilities in this case seem to improve with age. Female elephants travel around in small social groups led by a matriarch. These groups may meet up with a dozen or more other groups at different times while traversing the ranges of their habitat. To prevent hostilities and reduce possible stress or panic it is important for the elephants to know whether the groups they are meeting is a potential threat or not. Older matriarchs are obviously prized by poachers because of their large tusks, so now many social groups have unusually young matriarchs. Karen McComb found that the older matriarchs (55+ years old) were able to respond in these play back experiments with a greater degree of association between the calls they recognised and the exact degree of familiarity they had with the caller (McComb et al., 2001). Younger matriarchs were several thousand times worse at doing this (in terms of their calculated index of associativity). Although we can't be sure, it is likely that this advantage of age is due to more extensive experience and memory rather than some acuity advantage. It does however underline that there are some positive benefits of age and shows just what damage poachers may be inflicting on the social structure of the African elephant by killing off the main repositories of social knowledge!

Dolphins and "signature whistles"
Bottlenose dolphins are like elephants in that they live in fission/fusion societies in a small tight-knit social group that repeatedly comes into contact with other groups. They are thought to use "signature" calls as part of their social communication repertoire. The idea is that these calls convey primarily information about the identity of the caller. If you put it in a human language context it is similar to introducing yourself to me where you might say: "Hi, I'm Robert" and I would reply "and I'm Keith". Not only are these referential calls used to identify an individual but the caller can also imitate the signature of an individual whose attention it is seeking. In human equivalents this like saying: "Hey Keith, I'm Robert". Many regard this imitative step as the beginning of the fundamentals of complex language. It must be said however that this field is still somewhat controversial.

Play-back experiments in these dolphins have also established that a number of different individuals can be recognised but sample sizes have not been as large as in the elephant studies (10-20 or so). To confuse matters, recent work has seriously questioned whether dolphins really do use "signature" whistles or whether like other species their individual voices during routine communication are distinctive (McCowan and Reiss, 2001). However, this does not detract from the fact that they can recognise and imitate each other vocally.

Head turning monkeys
Most monkeys, like their human counterparts, are pretty good at distinguishing between the voices of different

individuals in their social group. Once again "play-back" experiments have been used extensively to establish this. Female monkeys have been found to successfully discriminate between the "coo" calls of their kin as opposed to non-kin so it is a good way of distinguishing relatives. As with dolphins the upper limits on numbers of individuals that can be recognised have not really been assessed for obvious logistical reasons. It is likely to be high however, particularly in tree-dwelling species, because visual identification may be difficult in dense vegetation.

An additional ability that has been demonstrated in vervet monkeys is recognition of third-party relationships using vocal recognition. In play-back experiments where the call of one mother's infant is played to the troop, many of them will look in the direction of the mother whose baby has called. Recognising and responding to relationships between other individuals is a very advanced level of social evolution (Cheney and Seyfarth, 1990).

A final interesting point is that monkeys show a right ear advantage for recognising the vocal calls (alarm calls or food calls) of familiar animals. When rhesus monkeys hear playback recordings behind them they turn to look over their right shoulder whereas if the voices are unfamiliar they either turn to the left or not at all (Hauser and Andersson, 1994). There is clearly a developmental sequence to this since infant monkeys do not show it. Because, like the visual system, the left side of the brain processes auditory cues from the right ear, this indicates that monkeys are mainly using the left side of the brain to recognise familiar voices. This may be the precursor for language specialisation in this brain hemisphere in humans.

The case of the laughing hyaena

The hyaena represents another non-primate species with a highly sophisticated social group organisation that would appear to demand individual recognition skills. Indeed, playback experiments have confirmed that mothers in this species respond differentially to the "whoop" calls produced by their cubs. There is also some indication that they can recognise the voices of other individuals within the clan. However, unlike monkeys, they showed no evidence for recognising third-party relationships (Holekamp et al., 1999).

Other species

Mothers and infants of a large number of other mammals have been shown to recognise each other vocally (for example sheep, cattle, deer, bats, seals, sea lions, manatees). Indeed it is likely that most mammals which communicate using vocalisations and dedicate their parental resources to small numbers of offspring have at least this ability since their protection is of paramount importance for promoting ones genes in subsequent generations.

What are the main cues for individual vocal recognition and how does the brain make the necessary distinctions?

There are a number of different sources of variability in voice sounds that could be used to determine individual identity. At the simplest level the fundamental frequency of the voice offers quite a range (high or low pitched etc). However, as with smell, the most informative component is in the patterning of the sounds rather than in any single component. Thus in monkeys playing the same call backwards makes it unrecognisable (Ghazanfar et al., 2001). This suggests that the temporal spectral patterning of voices is very important. Human voice recognition also relies heavily on these temporal aspects of speech sounds.

Compared to our understanding of visual or smell-based recognition systems in the brain we know much less about vocal recognition. Areas of the auditory cortex (superior temporal cortex) are clearly critical for this and in monkeys the left brain hemisphere is more important than the right for voice recognition but not for recognition of other types of sounds (Ghazanfar and Hauser, 2001). Cells within these areas have been shown to be particularly tuned to key temporal or frequency components of particular calls or to combinations and timings of frequency components (such as in the bat). However, to date, cells within the brain that selectively encode specific types of vocalisations, or the sounds of particular individuals, have not been reported although functional imaging studies of the human brain have reported voice-selective areas in the auditory cortex (Belin et al., 2000).

What are the limitations of recognising individuals by their voices?

While vocal recognition can be very useful for helping locate a specific individual who is some distance away it has one serious drawback. It relies entirely on another animal or human actually producing a vocal signal. Thus, unlike smell or visual cues which are produced constantly, vocal cues are brief and entirely under the control of the signaller rather than the receiver. So an animal that took on Trappist vows of silence would to all intents and purposes become invisible to others. It makes sense therefore that this is used more for alerting other individuals to your presence and communicating information or intentions to them over distances where other senses are ineffective. You need to know where an individual is that is calling to you and what they are saying but the most part you won't expect to be able to identify that many individuals from the sound of their voices alone. As humans we only have to think of how few people we can recognise instantly over the phone! However, to put this in context vocal recognition offers greater potential for identifying individuals than smell since with its greater neocortical representation in the brain it offers both greater computational processing availability and less direct associative links with emotional centres.

Individual recognition by sight

For humans and non-human primates we have developed our visual sense to such a degree that it is the most critical for recognising important things in the world around us. Social recognition is a prime example of this. Both we, and those of our primate cousins that are mainly diurnal and have good visual acuity in daylight, recognise each other mainly by visual cues. Not surprisingly, the face represents the best region to focus on because it has a number of features that vary to some degree between individuals. It is also the centre of both visual perception (through the eyes) and communication (through the mouth) and of course the other senses (nose for smell and ears for hearing) are also there. Faces can be used to convey emotions and intentions through changes in eye-gaze and facial expression. In short, pretty much everything you need to know about another individual comes from the face. As T.S. Eliott has aptly put it in his poem "The Love Song of J. Alfred Prufrock", when we go out we do indeed: "..prepare a face to meet the faces that you meet".

As humans we are all aware that we can recognise and remember many hundreds of individuals from their faces. It is not surprising therefore to learn that the primate brain has evolved special centres in the temporal lobe for the purpose of recognising faces as opposed to other sorts of visual object and that cells can be found in these regions that respond selectively to different faces. If this general region is damaged, or becomes dysfunctional for some other reason, in humans it can lead to a form of person blindness where individuals cannot be recognised from their faces even though other forms of visual object recognition are intact. This condition has been called "prosopagnosia" (i.e. difficulty with remembering faces). Difficulties with face recognition, and/or responding appropriately to facial expressions, can also be seen in schizophrenia and autism.

So what precisely is special about face recognition in humans?
• We can recognise and remember large numbers of different faces for a very long time
• We can learn to recognise a new face very quickly (often in a matter of a few seconds).
• Faces are a major source on individual attraction.
• We are very sensitive to internal configural differences in familiar faces (i.e. the relative positions of eyes, nose and mouth)
• We expect to see faces upright and have difficulty recognising then upside down (not a problem with landscapes or other types of objects).
• Our brains make lots of configural assumptions about how faces should look (The Thatcher illusion for example where if her face is viewed upside down but her eyes and mouth are kept the right way up our brains refuse to believe this and so the eyes and mouth appear to be inverted as well).
• When we imagine other people we tend to think of their faces.
• Special parts of our brain deal with visual cues from the face.
• These are mainly in the right brain hemisphere and so recognition is better for the half of the face appearing in the left visual field because this information is processed mainly by the right side of the brain.
• When we imagine a person's face a similar pattern of activation occurs in this brain region as when we actually see it.
• The brain face recognition system requires a considerable period of experience to become fully expert (10-12 years).

Although a fair amount of work has been done to establish individual face recognition skills in chimpanzees and some macaque species it is not an easy task. Differential behavioural (usually vocalisations or threat) responses or abilities to match faces have often been used. In face matching tasks Chimpanzees could do this for 50 different examples of unfamiliar faces (Parr et al., 2000). While similar areas of the brains of macaques, and presumably other non-human primates, appear to be specialised for processing faces are seen in humans there is relatively little definitive evidence that the right side of their brains are used more than the left. However studies in Chimpanzees have revealed some support for their using the part of the face appearing in the left visual field more for both face recognition and recognition of face emotion (i.e. such cues should be mainly processed by the right side of the brain).

There has always been an assumed hypothesis that the development of specialised face recognition skills is a feature of primate social evolution. Indeed, on the face of it (if you excuse the pun!) such an argument seems very reasonable. It has also been argued strongly that the specialisation in humans for face recognition in the right hemisphere may have simply arisen because the evolution of human language took over the same area of the brain in the left hemisphere. During the last 18 years I and my colleagues have been involved in showing that neither of these two hypotheses is correct by considering the face recognition skills of what would appear on the surface to be a most unlikely candidate non-primate species of mammal, the humble sheep.

The story of sheep face recognition
The story started when I arrived at the Babraham Institute in 1983 to work on the control of sheep maternal behaviour. Three important pieces of information struck me as suggestive of the possibility that sheep could recognise faces. In the first place they had remarkable visual acuity that allowed them to distinguish visually between a whole range of different types of grass, clover and food concentrates. In the second place a previous researcher at the Institute, Elisabeth Walser, had reported that mother ewes had trouble recognising their lambs if she placed artificial colourings just on their heads but not on other individual body regions. Lastly, sheep had a highly evolved neocortex including the same general region of the temporal cortex reported to important for face recognition in humans and monkeys.

In 1985 we started to establish if this region of the brain had cells specialised for responding to visual images of faces – an ambition which very few of my primatologist colleagues could take seriously. In 1987 the results were published in the journal Science (Kendrick and Baldwin, 1987). Not only did sheep have these specialised cells but they could be shown to divided faces up into emotionally distinct categories (whether faces had horns and how big they were – an important index of dominance and gender; whether faces were of members of the same breed and how familiar they were – sheep prefer the company of their own breed and are known to strike up long-term individual friendships; whether faces were from species that could pose a threat – humans and dogs). The cells respond very quickly (usually in less than 100 msec) which is faster than it is possible to make any behavioural response to what is being seen. This may explain why we, and sheep, often move automatically towards an individual that looks familiar only to find that they are not after all. Alternatively, the sight of a face resembling that of your boss, or an enemy, may trigger immediate evasive tactics without cause! This face recognition system in sheep is mainly designed for identifying categories of individual that have a specific emotional significance. It implies close interactions between the brain systems dealing with detection of faces and those associated with making emotional responses. Interestingly it is often just this link that appears to break down in individuals with schizophrenia and autism. The system is also optimised for speed and this results in an accuracy trade-off. This makes sense from a survival point of view because if there is a chance that you might get eaten, or beaten up by, another individual it is better to optimise the speed with which you escape from them even if you get it wrong from time to time (better embarrassed at being wrong and alive, than chuffed at being correct but dead!).

Over the next years we set about the task of showing systematically whether sheep could distinguish between categories of individual and then the extent to which they could actually identify specific individuals from their faces. The first step for doing this was to construct a choice maze apparatus that allowed sheep to choose between face images in order to gain access to the real individual whose face-picture had been seen. To do this we gave the sheep pairs of faces that had different attractions to them (i.e. sheep vs human; familiar vs unfamiliar animal or breed; male vs female). If the sheep normally used faces to distinguish between categories of individuals we argued that they would not have to learn to do this task and would always chose the face that was most attractive to them. This is exactly what happened. The sheep chose sheep faces over human ones and familiar sheep faces over unfamiliar ones. We mainly used female sheep for these studies and they showed a clear ability for distinguishing gender. When they were not sexually interested in males they chose female faces every time, but switched to choosing male faces for a couple of days during each cycle when sex was on the agenda. They even showed some preliminary evidence for individual recognition by actually having preferences for the face of one male over another (the media referred to this as a kind of sheep dating agency!). Interestingly, more mature males seemed to get the vote over younger ones! (Kendrick et al., 1995). So being an old ram or goat may have its compensations. In any event, face cues are clearly being used for attraction as well as recognition in sheep and we confirmed this again in studies we carried out establishing that mothers particularly influence the female facial characteristics that their male offspring found attractive when they grow up (Kendrick et al. 1998) (Ma Ma's Boys as one paper put it!).

Sight of familiar faces also has a profound calming influence on sheep experiencing the psychological stress of a brief period of isolation. A familiar face reduces behavioural expressions of stress (vocalisations and increased activity), autonomic indices (heart rate), hormonal indices (adrenalin and cortisol increases) and activation of areas of the brain controlling stress and fear responses.

To establish the full extent of individual face recognition powers of sheep we had to use faces of the same breed and sex and that had more equivalent levels of attraction. In this case it was necessary to reward the animals for making a correct choice by giving them food and they obviously had to learn which of the two face pictures got them the reward. We used the same choice maze for this and also a more sophisticated apparatus where the animals indicated which of the two pictures they had chosen by pressing one of two different panels with their nose. This allows us to use computer technology to systematically alter the appearance of faces either by showing missing, selective or rearranged features or by blending two faces progressively into one another using morphing programmes so that we can assess how good they are at telling two faces apart. In all cases the face pictures were edited so that no other part of the body was shown we also used the same kinds of digital editing techniques commonly used in fashion magazines to remove some unwanted features (such as ear tags, just in case the sheep were reading the numbers!). Using these approaches we have established the following facts about sheep face recognition:

• Both sheep and human faces can be discriminated.
• Sheep are better at recognising sheep than human faces (the opposite is of course the case for humans!)
• Up to 50 different sheep and 10 human faces can be discriminated at any one time (probably many more).
• Faces can be remembered for over two years.
• Face discriminations can be learned faster than for simple geometric symbols like squares, circles and triangles.
• Inverted sheep or faces, but not other objects, are difficult to recognise.
• Sheep faces are learned faster than human ones.
• Familiar faces can be recognised just using the internal face features
• Shearing does not impair face recognition
• You don't recognise a face by its horns
• Cues from the part of the face in the left visual field are used more for recognition than those in the right (i.e. implies a right brain hemisphere advantage for faces).
• The eyes are the most important single feature for recognition
• For sheep faces a 15-20% difference in appearance is required for accurate discrimination (humans can detect a 10-15% difference doing the same task)

- For human faces sheep are not so good (20-25% difference required) compared with (5-10% for humans).
- Faces can be discriminated down to about 25% of normal size.
- Lambs take a number of months to learn how to recognise faces.

Does the sheep brain recognise faces the same way as the human one does?
Clearly the behavioural studies, together with the initial brain cell recording work, suggest that there are remarkable similarities between sheep and human face recognition. In support of behavioural indices of long-term memory for faces, cells in the temporal cortex which respond to specific sheep or human faces have been shown to retain this capacity even when the individuals concerned have not been seen for more than a year (Kendrick et al., 2001). As with the human brain the medial prefrontal cortex and parts of the amygdala are also involved in processing faces.

We have also confirmed that the temporal cortex on the right side of the brain is more strongly activated by faces than the left although the left does respond to faces, but much more slowly (by nearly 400 msec in some cases - implying that it is involved in something other than immediate recognition)(Peirce et al., 2000; Peirce and Kendrick 2002). This combined with our behavioural work surely kicks into touch the idea that right brain hemisphere dominance for face processing in humans is the result of language taking over the left hemisphere – unless of course we are proposing that sheep have evolved language skills similar to our own!

Can sheep also imagine faces?
So if sheep have similar specialised systems within their brains for recognising faces as us and we can use these same systems to imagine faces, can sheep do the same? Preliminary answers to this would suggest that indeed they can, at least to some limited extent. How can we show this? Well it is by no means a simple question to address but we have taken three different approaches (Kendrick, Leigh and Peirce, 2001):

Behavioural tests: A simple behavioural approach involves firstly establishing that the animals can remember where faces were even when they are screened for 10-15 seconds. A more sophisticated approach is rather like a game of "SNAP" where the animal needs to remember a face that it has seen previously in order to indicate which of two faces shown subsequently matches it. Some animals can do this too. Another way of testing the potential for using mental imagery is to train the animals to discriminate between pairs of familiar or unfamiliar faces from the front and then suddenly switch the images used to profile views (or vice versa). The sheep continue to get the task right when the face views are changed. This shows both that they know it is the act of recognising a particular individual rather than a particular view of their face that gets them a reward (i.e. true individual recognition) and that they may be able to mentally rotate the image of the face from front to profile in order to match a front view with a profile one.

Imaging activity changes in brain areas involved in face processing: We know that some of the main areas involved in responding to visual images of faces in the sheep do not respond to smells or vocal sounds. Sheep can recognise individuals from their voices or smells and so one simple question is whether for example hearing the voice of your lamb triggers your brain to form a mental visual image of its face. This would appear to be just what happens and only if the voice is recognisable, not for example if the same components of the voice are played but in a jumbled up sequence.

Activity of cells in face-processing areas: The final piece of evidence one can provide is that cells in the brain which respond selectively to the sight of the face of a particular individual do so even when that individual is not there. To do this the cells need to be recorded from while the animal sees video sequences which reveal the presence of an individual behind a tree or in a pen. The animal being recorded from is then shown a slightly different film sequence but the familiar individual it is expecting to see is no longer there. In this case the cells are activated at the point where the individual is expected to appear even when they do not.

So the bottom line is that sheep have similar face recognition skills to identify individuals as we do, and can probably even imagine the faces of individuals in their absence. Recognising individuals from their faces is clearly not just a feature of primate evolution and our sheep work opens up the possibility that other mammals with good visual acuity may have similar abilities (horses, goats, cattle, dogs for example). If we equate the presence of complex individual recognition skills with superior intellect this may leave us feeling slightly uncomfortable in considering sheep, or indeed other non-primate mammals, in this category. While it is clear that other challenging aspects of social and physical environments also act significantly to shape the evolution of intelligence, it has to be said that social recognition skills of the kind we have found in the sheep demand a radical re-think of what they are actually capable of. This serves as an important reminder that casual observations of the behaviours of some animals that are naturally fearful and apparently guided by a mindless group-dominated mentality can result in misleading conclusions about their abilities.

Can sensory information be combined to effect more accurate recognition?
Behavioural studies in humans and some animal species clearly indicate that having simultaneous information from different sensory modalities can improve the accuracy of identifying individuals, particularly under difficult circumstances. From our own work on sheep we have also found that pairing a sheep face paired with the wrong voice can impair recognition accuracy. How information from different sensory modalities combines to aid recognition is less well understood since each sensory system has its own specialised areas to process the necessary cues to establish identity. One area that is particularly important is the frontal cortex and here we have found, for example, cells that respond both to the faces of specific individuals and also to their smells. Of

course all the different sensory systems access the same behavioural response control regions of the brain (including the frontal cortex). So it is still possible for additive accuracy effects of multi-sensory cues to occur relatively independently through their combined influences on triggering the particular motor components of a specific behavioural response (escaping from or approaching a particular individual for example).

Some general final conclusions

Other animals can certainly recognise and remember individuals by their smell, voice sounds or faces.

In general they are better at recognising their own species than others.

This is because the task is so difficult it requires the sense organs and the brain to adopt a complex pattern recognition approach which is optimised for processing the signals provided by members of your own species.

Remembering lots of different individuals therefore requires considerable amounts of grey matter!

Perfume is not an aid to identity or a means of deception – at least not in other animals!

Elephants and dolphins don't forget a good voice.

If you speak to someone from behind and they turn to look at you over their right shoulder they may well have remembered who you are.

While smells and voices can be good for recognition, faces are even better.

Remember it's the right side of your face (on the left of the person looking at you) that gives the main key to your identity and emotional state.

We may not be the only species capable of imagining the faces of our friends and enemies.

So you thought sheep all looked alike and lacked a brain. Face up to it, you need to think again!

Some selected references:

Belin P et al. (2000) Voice-selective areas in human auditory cortex. Nature 403:309-312.
Cheney DL and Seyfarth RM (1990) How monkeys see the world. University of Chicago Press, Chicago.
Ferguson JN et al. (2000) Social amnesia in mice lacking the oxytocin gene. Nature Genetics 25:284-288.
Ghazanfar AA and Hauser MD (2001) The auditory behaviour of primates: a neuroethological perspective. Current Opinion in Neurobiology 11:712-720
Hauser MD and Andersson, K (1994) Left hemisphere dominance for processing vocalizations in adult, but not infant, rhesus monkeys: field experiments. Proceedings of the National Academy of Sciences USA 91:3946-3948.
Holekamp KE et al. (1999) Vocal recognition in the spotted hyaena and its possible implications regarding the evolution of intelligence. Animal Behaviour 58:383-395.
Janik, VM (2000) Whistle matching in wild bottlenose dolphins (Tursiops truncates) Science 285:1355-1357.
Kendrick KM and Baldwin BA (1987) Cells in the temporal cortex of conscious sheep can respond preferentially to the sight of faces. Science 236:448-450.
Kendrick KM et al. (1992) Changes in the sensory processing of olfactory signals induced by birth in sheep. Science 256:833-836
Kendrick KM et al. (1995) Facial and vocal discrimination in sheep. Animal Behaviour 49:1665-1676.
Kendrick KM et al. (1998) Mothers determine sexual preferences. Nature 395:229-230.
Kendrick KM et al. (2001) Sheep don't forget a face. Nature 414:165-166
Kendrick KM, Leigh A and Peirce J (2001) Behavioural and neural correlates of mental imagery in sheep using face recognition paradigms. Animal Welfare 10:S89-101.
McComb K. et al. (2001) Matriarchs as repositories of social knowledge in African elephants. Science 292:491-494
McCowan B and Reiss D (2001) The fallacy of 'signature whistles' in bottlenose dolphins: a comparative perspective of 'signature information' in animal vocalizations. Animal Behaviour 62:1151-1162.
Parr LA et al. (2000) Recognizing facial cues: individual discrimination by chimpanzees (Pan troglodytes) and rhesus monkeys (Macaca mulatta). Journal of Comparative Psychology 114:47-60.
Peirce JW and Kendrick KM (2002) Functional asymmetry in sheep temporal cortex. NeuroReport 13:2395-2399.

Peirce JW, Leigh AE and Kendrick KM (2000) Configurational coding, familiarity and the right hemisphere advantage for face recognition in sheep. Neuropsychologia 38:475-483.