Human and animal emotions: Are they the same?

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"To understand, as far as is possible, the source or origin of the various expressions which may be hourly seen on the faces of the men around us, not to mention our domesticated animals, ought to possess much interest for us."

Charles Darwin "The Expression of the Emotions in Man and Animals" (1872).

Darwin 's view in this book on emotions was largely ignored in his day although it seems to be undergoing something of a revival. He clearly expresses in this book the idea that emotions are subject to the same processes of evolutionary adaptation as other behavioural and physiological traits. Proof of this is a problem since it is very difficult to establish what another human is thinking or feeling let alone what a member of another species is experiencing. His book therefore represents a somewhat observational attempt to illustrate the expression of emotions in other species as well as humans. He concludes by saying that what is needed is a more physiological approach:

"… the philosophy of our subject has well deserved the attention which it has already received from several excellent observers, and that it deserves still further attention, especially from any able physiologist."

A number of more recent attempts at establishing the presence of emotions in other animals have also focussed of providing a wide range of observations of animal behaviour highly suggestive of emotions being experienced. These include Jeffrey Masson and Susan McCarthy "When Elephants Weep" (1994) and Marc Bekoff "The Smile of a Dolphin: Remarkable Accounts of Animal Emotions" (2000) and "Minding Animals: Awareness, Emotions and Heart" (2002).

Most humans who come into regular close contact with animals have little trouble in answering "yes" to question of whether other species can experience similar emotions to us and the examples given in the above books can be highly persuasive. I spent a considerable portion of my last lecture on communication in humans and other animals showing that the majority of what we and they communicate to one another is mainly emotional state and immediate desires through body language, expressions and vocalisations. It therefore comes as a big surprise to many when they hear that a good number of behavioural scientists either chose to ignore the subject of animal emotions or even dispute the very existence of human-like emotional experiences in other animals. This lecture will try to provide an explanation of why both sides in this controversial and often heated argument can be right.

Definition of Emotions

The first problem that needs to be faced when considering emotions is defining what they are exactly. Definitions can be quite wide ranging because the word actually covers a multitude of complex physiological and mental processes. A typical dictionary definition is:

“A moving of the mind or soul; excitement of the feelings, whether pleasing or painful; disturbance or agitation of mind caused by a specific exciting cause and manifested by some sensible effect on the body” (Webster)

A further problem one encounters on investigating what is known about human emotions is that there is not even a consensus view about how many there are or which, similar to primary colours, are the primary emotions from which all others derive. On the one hand we have claims that humans can have up to 100 different emotions while on the other we have a number of researchers concluding that there are only between four and eight primary ones. The only problem with the latter is that there is not great agreement as to which ones qualify as primary states! Most agree that primary emotions should be associated with specific and relatively invariant physical displays. Some (Paul Ekman) have argued on the basis of distinct human facial expressions for the primacy of surprise, happiness, anger, fear disgust and sadness while others (Robert Plutchik) have extended this to cover other bodily expressions including acceptance and anticipation.

Most of us would probably be happy to opt for a classification of emotions that was in the form of a series of dimensional continuums with, for example “happy” being at one end and “sad” at the other but that also, like a primary colour chart, allowed for mixing to take place to create all the other secondary or even tertiary emotions. Robert Plutchik has attempted this. His idea is that eight basic emotions can be arranged in a circle and be mixed as dyads. The further away the emotions are in the circle the harder they are to mix. Adjacent emotions (primary dyads) are for example friendliness which derives from mix of joy and acceptance and alarm which derives from a mix of fear and surprise. Examples of a mix of emotions one removed from each other (secondary dyads) are “guilt” derived from joy and fear and “sullenness” derived from sadness and anger. Examples of a mix of emotions two removed from each other are “delight” derived from joy and surprise and “anxiety” derived from anticipation and fear. By the time you get to three removed from each other it is pretty clear that there is little opportunity for mixing because they are effectively opposites (i.e. joy and sadness, fear and anger, disgust and acceptance, surprise and anticipation) (Plutchik, 1980).

However, the main purpose of this lecture is not to try to classify all the different human emotions and how they are related to one another. There is no doubt that human emotional repertoires are far more complex than those present in other species in the same way as for cognition and consciousness. I will therefore confine myself to a number of fairly basic emotions and examine whether their expression is the same in other species. To this end I will focus on fear, anger, disgust, jealousy, sadness, shame, joy and love, and some of their derivatives.

First however we need to consider in a little more detail what emotions are and what function(s) they actually play:

What are emotions and why do we have them?

As far as humans are concerned our emotions are associated with a variety of different pleasant and unpleasant feelings evoked either by external events or that can be self-generated by our thoughts. Because emotional states have a profound effect on our peripheral nervous system (racing heart rate, changes in blood pressure and blood flow to the internal organs, muscles and skin, sweaty palms etc) it was originally proposed by William James that the different feelings we experience are mediated by the effects that different patterns of changes in the body mediated by the peripheral nervous system and hormones. However, it is now clear that there is a great deal of overlap between the peripheral effects of different emotional states and that in many cases “feelings” are experienced before such peripheral changes have even occurred. The different feelings we experience in the context of our emotional responses are therefore down to the way the brain is interpreting different situations and this is reflected by all subsequent theories of emotional function. This interpretation in humans is strongly influenced by our use of language since we use it both to label and define a variety of slightly different emotional responses.

In essence a generic emotional response can be seen as specific sensory cues (or thought processes) which elicit an emotional response (a defined set of behaviours, further attention to these cues), leading to an emotional state (bodily changes typified by enhanced arousal – including altered heart rate and blood pressure, altered blood flow to skin muscles and internal organs) leading in turn to positive or negative feelings associated with these changes.

So what makes us feel “good” or “bad” when we experience different emotional states? The answer to this was first provided by experiments involving electrical stimulation of the brain in rats by James Olds in the 1950s and subsequently confirmed in humans. Olds found that when electrodes were placed in certain regions of a rat’s brain that they would incessantly press a lever in order to deliver electrical stimulation into them with no other apparent reward. Lever pressing rates could go above 6000 times per hour and animals faced with a choice between stimulating these brain regions and alleviating hunger they would actually starve themselves! Furthermore, there does not appear to be a satiety mechanism involved in this pleasure system. Subsequent experiments on human patients in the USA by Dr Robert Heath and others have confirmed that these same regions produced the self-stimulation behaviour in humans and that the humans doing this reported feelings of intense pleasure. Following on from this other brain regions were discovered where aversion/pain responses were activated.

The brain regions that are associated with “pleasurable” experiences are also activated by a wide range of drugs, which is why their effects can not only evoke positive emotional experiences but can also, be highly addictive.

For some time it has been thought that “pleasure” and “pain” centres in the brain were distinct, even though our experience of them may have often suggested to us that there could be some overlap. A recent brain imaging study in humans has now shown that pleasure and pain do to some extent co-activate brain regions traditionally thought to play roles in one emotional experience as opposed to the other. When human subjects had heat applied to their hand through a heat pad it was found that hot temperatures activated both the classic pain circuitry of the brain and pleasure areas (Becerra et al. 2001). The philosophers Spinoza and Bentham who proposed that pleasure and pain were part of the same spectrum appear therefore to have got it right!

It is important not to conclude from this that “feelings” of pleasure and pain are mediated entirely by these primitive sub-cortical structures in the brain. Such feelings are conscious and must therefore rely on output from these more primitive structures feeding back to the brains mediator of consciousness – the neocortex.

The important conclusions that can be drawn from these experiments are that: (1) positive and negative emotional states can be generated by electrical activity in certain regions of the brain and (2) that many of the regions of the brain concerned are mainly ancient in terms of evolution and are largely conserved from reptiles through to mammals (i.e. it is not so much the “thinking” neocortical regions that generate “emotional states” per se but the lower more ancient structures which they can, of course, influence through their connections with them) (3) Feelings experienced as a result of the activity in these primitive brain centres are primarily mediated by the conscious parts of the brain i.e. the neocortex.

Because emotion seemed to be mediated mainly by primitive structures in the brain these brain circuits were defined as the brain’s emotional system and called the “Limbic Brain”. The involvement of the neocortex was largely ignored and with a further assumption (which was wrong as it turns out) that cognition and consciousness were controlled by the brain neocortex, Psychologists from the 1960s onwards have mainly focussed on cognitive functions and considered emotion to be totally separate from this. A horrible mistake as it turns out and one that set back work on how emotions are controlled considerably. We now know of course that our different emotional states and feelings can have a widespread influence on every aspect of cognitive function from attention through to memory (see the books by Le Doux and Damasio in the references below). I would go as far as concluding that:

"If cognition provides us with the building blocks of life and how they can be organised, emotions are often the cement that binds them together into permanent structures".

What can be tentatively concluded from the above arguments is that a huge number of different animal species must have the capacity to experience positive or negative emotional states although when, where and for how long this experience occurs is usually very much dependent on the way that the "thinking" parts of our brain function. For this reason the same cues from the environment can be given different emotional interpretations. A baby seeing a jack in the box open for the first time may either start laughing, or cry or simply be confused. In the same way we must not therefore make the mistake of assuming that what generally makes us feel happy or sad will have the same effect on another animal species.

What functions do emotions serve?

One of the most important survival mechanisms for all animals is to have an optimal "fight" or "flight" response strategy. To be most effective this should be virtually completely automatic since any involvement of a time consuming "thinking" component would probably end up with you being dead. Such life or death situations are of course associated in humans with strong negative emotional states and feelings. However, we experience them primarily as a consequence of our actions in response to emotional cues, they are not therefore necessary for driving the response itself. For example, you only experience fear as a result of a snake launching a strike at you after you have reared back to avoid being bitten by it. The feelings that we experience in these emotional circumstances are those that impinge on our consciousness and if we had to wait for this to happen before we could avoid the snake we would have been far too late to avoid the bite!

The dissociation between behavioural aspects of emotional responses and conscious experience of "feelings" associated with them is effectively the main argument used to postulate that it is not essential for other species to "feel" conscious reactions to stimuli that evoke emotional responses. Simply stated, the point being made is that other animals may be able to exhibit all the same behavioural signs of human emotions without necessarily being able to experience the conscious "feelings" associated with them. This idea allows one to maintain a view that other animals both do not need to have a capacity for consciousness and cannot experience suffering.

If we go along with this line of reasoning for a moment then the obvious next question is what additional purpose is served by humans experiencing feelings as a consequence of their emotional reactions. One obvious answer to this is that the experience of these feelings can, in particular, give us even better adaptive advantages for learning about and controlling events in our all important social environment. Humans who as a result of brain damage, or developmental (autism), psychological (schizophrenia, depression) or neurodegenerative (Alzheimer's and Parkinson's diseases) experience problems in interpreting and responding to emotional cues or experiencing "feelings" have enormous problems in dealing with social contexts. Since the majority of social animals have the same issues of integration into complex societies it is difficult to see how they would not have evolved the same brain mechanisms to allow them to experience feelings to help guide them in such social contexts.

Quite apart from the importance of emotions in a social context however is the amazing influence emotional experiences can have on learning. Indeed, how Psychology ever considered cognition as being totally separate from emotion is perplexing and perhaps owes much to the conception of man as more of a thinking rational organism than as an irrational one totally dominated by primitive drives and emotional reactions.

Most things we have to learn in life require some degree of repetition to be retained for any length of time.

However, things that we are exposed to that either evoke a strong emotional reaction, or just happen to be around at the time, tend to result in immediate and relatively indelible memories that may even last a life-time. Thus complementing our simple emotional reactions to events with feelings provides us with even more flexibility in using our emotions to help remember things. Also, the pairing of conscious feelings with conscious thinking and planning processes allows us both assess the likely consequences of our planned actions more effectively and even to remember the stages in a complex sequence of them. Adding language to this scenario massively enhances this potential.

The case of Alexithymia

A number of human psychosomatic (for example panic and post-traumatic stress disorders) and personality disorders are associated with an inability to recognise, experience and describe feelings. People with alexithymia tend to avoid internal emotional conflict by relying on action to express emotion which can often take the form of harming themselves. Recent brain imaging studies have shown that such individuals have reduced activation in a number of areas of the neocortex in the right brain hemisphere (notably in the frontal cortex) in response to viewing angry and sad faces (Kano et al, 2003). Thus the interpretation of emotional responses in terms of feelings does seem to involve higher areas of the brain that have increased disproportionately in size in the human brain compared with other species. We should therefore be careful not to conclude too quickly that animals can experience and identify the same range and quality of “feelings” as we can even if they possess a similar representation of the “older” brain structures that mediate emotional responses and the basic components of pleasure and pain.

However, the consequences of Alexithymia in humans may be instructive when considering other animals. It is easy to conclude that the build up of emotional reactions is like a pressure cooker that humans can release through experiencing and interpreting feelings as well as by action. With humans at least, if one can’t interpret feelings the kinds of actions used to help release emotional pressure can be quite self-destructive. Other animals often show self-mutilation or destructive tendencies which could be interpreted as a way of releasing their emotional pressure cookers because they have limited abilities to experience and interpret feelings associated with emotional states. On the other hand one could argue that this type of action should therefore be relatively universal in most animals at some stage in their lives, whereas it does not really seem to be so, at least in adults. So perhaps many other animals must have some limited capacity to experience feelings to help deal with interpreting their emotional pressure cookers and the ones who aren’t too good at this end up like human alexithymics. This is of course total speculation.

In the next sections I will look briefly at some key different human emotions, what we know about their control and the brain regions involved. I will also try to give some examples of where similar emotions may be being expressed by other species. It is important to emphasise that Wittgenstein’s caveat about likely differences between human language and any other language which might or might have been developed by another species: “If a lion could talk, we would not understand him” also applies in the context of emotion. The sensations that promote the experience of emotion, the nature, intensity and duration of the feelings experienced and ways that such experiences are communicated to others are likely to be highly species specific.

Fear

Everyone agrees that fear is a basic emotion and fear responses are displayed by a wide range of different species. We also know more about the control of this emotion in man and other animals than any other. Joseph Le Doux, in particular, has produced a large body of work exploring control of fear in laboratory animal models as well as in humans and which he has described in several popular science books (see “The Emotional Brain”, 1994; “Synaptic Self”, 2002).

The fear response is a highly important survival tool for most animals. The act of freezing or running when fear-evoking cues are detected is a highly effective biological defence mechanism. However, as I have already indicated when you detect and respond to cue that makes you fearful, it is not the experience of fear that makes you respond (i.e. you don't run from the bear because you are afraid, you are afraid because you are running from the bear).

The basic fear processing system in the brain appears to be remarkably conserved from reptiles through to humans. For many animals, including humans, some cues appear capable of automatically evoking fear responses. We, along with many other mammals, automatically rear away from a striking snake even if we know that there is a solid plate glass window in between us and them. Birds will take immediate escape action when they see the silhouette of a bird of prey but not of other types of bird. Many animals, including humans, freeze in response to fear-evoking stimulus since this has clearly evolved as a successful method of avoiding attracting the attention of a nearby predator. This kind of response did not of course cater for the advent of the motor car and so rabbits, foxes or deer freezing on the road in response to an on coming car are effectively using the wrong escape strategy but it is so hard wired that it is difficult to override. The kinds of sensory cues involved in evoking these responses are routed directly though to the parts of the brain dealing with fear reactions and are relatively inflexible in terms of modification by experience. However, as one would expect, if an animal is going to survive in a changing environment it is necessary to have some flexibility in learning what things to avoid.

The brain fear system is therefore a very good learner and it often takes only a single experience where an object or individual is associated with a life threatening/painful outcome for it to evoke a full fear response the very next time you encounter it. The memory associated with this may persist for many years, or even a life time, in some circumstances.

Numerous researchers, starting with Pavlov, have shown that an animal exposed to a stimulus, such as a tone, that is followed by an aversive experience, like an electric shock, learn rapidly to show both avoidance and "fear" responses to that predictive stimulus alone. This is classical conditioning and involves a conditioned stimulus (a tone or light) becoming associated with an unconditioned stimulus (a shock or loud noise for example) to evoke a conditioned fear response (salivation, change in heart rate, avoidance behaviours etc). Animals also quickly learn to associate other contextual cues with the fear experience such as the room or chamber where the experiments are being conducted and these can also subsequently evoke fear responses on their own even in the absence of the specific conditioned stimulus.

Whether we are talking about a lizard, a bird, a rat, a sheep and monkey or a human this fear system appears to involve the same brain areas and the same types of responses. Thus fear evoking stimuli cause freezing, changes in heart rate and blood pressure (autonomic) and in stress hormones (release of adrenocortical hormone from the pituitary which in turn releases cortisol from the adrenal gland). The autonomic and endocrine changes together put the body in a state of being highly prepared for action with the muscles, in particular being pumped up and primed for immediate action and all non-essential bodily processes shut down.

Joseph Le Doux in the USA has made extensive studies of the brain structures and pathways involved and the key region for the control of behavioural, autonomic and hormonal responses is called the amygdala. As its name suggests, this is an almond shape structure near the base of the brain within the temporal lobe and is phylogenetically old and well conserved across species- probably even the dinosaurs had this brain region. If this region is removed animals cease to show behavioural, autonomic or hormonal fear responses and although they are excessively tame they also have social and sexual interaction problems, problems with visual recognition of objects and are hyper-oral (investigate all kinds of objects with their mouths) and hyper-phagic (eat too much). This was first observed in monkeys and has been termed the "Kluver-Bucy" syndrome after the researchers involved. This has now been confirmed in a wide variety of other animals and even in humans who have undergone surgery for the prevention of uncontrollable epilepsy.

Conversely, electrical stimulation of this region provokes fear responses and humans report feelings of foreboding and imminent danger. The amygdala is a complex structure and is interconnected with sensory processing regions, hypothalamic areas dealing with motivational behaviours and hormone release and brainstem regions controlling autonomic responses such as heart rate and blood pressure.

We now know that sensory stimuli are relayed via thalamic nuclei to the lateral nucleus of the amygdala which integrates this information and sends it to the adjacent central nucleus. This latter nucleus has all the important connections with the hypothalamic, brainstem and motor control regions controlling fear responses and without this nucleus or the lateral nucleus such responses simply don't happen.

As one might predict, there are two different routes by which sensory information can reach these all important amygdala nuclei – a direct, fast and relatively undiscriminating one and an indirect slow and more discriminating one. The former relays sensory information from the eyes and ears via the thalamus directly to the amygdala and does not involve the conscious thinking parts of the brain (the visual and auditory processing parts of the neocortex for example) which are also better at discriminating between objects with similar sensory properties (a curved stick as opposed to a coiled snake for example). In a rat it takes around 12 milliseconds for information to hit the amygdala via this direct path. If it goes instead via the indirect path it can take 2-3 times as long. The way the system seems to work is that anything that resembles an object that is associated with immediate danger will hit the amygdala via route one and start off the cascade of fear responses. If it turns out that the additional processing available in the slower processing pathway shows that this is a mistake, and calls a false alarm, then this system can over ride the response cascade initiated by route one. Thus the fear system is optimised for speed or response (which optimises survival) but has some flexibility for interrupting it when a mistake is made.

Le Doux and others have also shown that the learning process whereby a novel stimulus comes to evoke a fear response also critically involves the central and lateral nuclei of the amygdala rather than other brain memory systems – although the latter may become involved in more complex discrimination or learning situations.

Faces and fear

In humans observations in individuals with damage to the amygdala and from brain imaging studies have shown that this region in the right brain hemisphere is important for recognising and responding to fearful or angry facial expressions. In monkeys work has also shown that the activity of cells in this region is sensitive to such facial expressions.

In sheep we have looked at the behavioural, autonomic, hormonal and brain changes that occur when an individual is exposed to a brief period of fear and anxiety caused by social isolation. As would be expected from work on other species this causes the animals to show behavioural signs of anxiety and fear (more protest vocalisations and restless moving about), as well as increased heart rate and blood levels of the stress hormones cortisol and adrenalin (produced by the adrenal gland). In the brain, the areas of the hypothalamus that regulate stress hormone responses are activated as are the fear centres in the amygdala (the central and lateral nuclei). However, if the animals are simply shown pictures of the faces of other animals of their same breed the areas of the brain that process faces are extensively activated (involving large parts of the neocortex) and all the behavioural, autonomic, hormonal and brain changes associated with fear and anxiety disappear.

Whether the animal really experiences the feeling of fear in the same way as we do is still difficult to assess. However, since there is an extensive involvement of the cortical "thinking" parts of the brain in being able to reverse the animal's emotional state it does suggest that the comforting effects of seeing a friendly face may be a positive conscious experience that is modulating a negative conscious feeling of fear. The idea of an evolutionary progression of neocortical influences on the activity of older structures mediating emotional responses is supported by observations that the level of connectivity between the cortex and limbic system regions such as the amygdala is considerably increased in monkeys compared with animals like rats.

Effects of constant anxiety

One of the most significant life stressors in social animals is being at the bottom of the dominance hierarchy. Social stressors of this kind can lead to an almost permanent state of anxiety in humans and are associated with elevated concentrations of stress hormones such as cortisol and the development of heart problems and ulcers. Interestingly, almost identical problems can be seen in apes and monkeys that are under constant social threat. In some New World Primates, like marmosets, subordinate members of the social group cease to show reproductive cycles as a result of elevated levels of stress hormones. It is tempting to speculate therefore that these animals are feeling the conscious effects of "anxiety" in a similar way to us. If they were not it is difficult to see why they would develop precisely the same disorders as us, especially when is clear that the main debilitating effect of anxiety is through having it as your predominant conscious feeling and being unable to control it.

In monkeys and some other animals, tranquilising drugs such as benzodiazepines (diazepam) and opioids also have the same fear/anxiety alleviating effects as seen in humans. The frontal cortex of the brain in particular seems to exert an important modulatory control of fear and anxiety responses and individual differences in sensitivity towards displaying these emotions. It is likely that this is the major brain site where many of these drugs act.

Anger and jealousy

As with fear most people consider that anger or rage responses are expressed widely in mammals. Like fear, anger has clear survival enhancing value in that it promotes aggression to obtain things that you want but for some reason can't get or, for example, can increase the ferocity of your aggression towards a combatant who has superficially injured you. It is also important to be able to communicate your state of anger to others since this will hopefully help to persuade them to give you what you want or to back off without further action being required.

Animal studies have shown that a number of areas of the limbic system (septum and amygdala), parts of the hypothalamus and the brainstem (i.e. all subcortical structures) can evoke anger/rage responses.

As with fear, the frontal cortex appears to play an important role in controlling anger responses through its connections with these subcortical regions.

Not surprisingly, little is know about how brain control of jealousy may differ from that of anger. The experience of the former often leads to the expression of the other. Most work focuses on sexual jealousy and I have seen plentiful evidence for behaviour that equates to this in other animals. I once spent several hours in London Zoo watching a dominant male timber wolf constantly hound a subordinate male every time he attempted to mate with his partner. His own partner was not in heat and so if he could not mate with her he was not going to let anyone else have sex. Wolves tend to pair with specific partners and so he made no attempt to have sex with the partner of the subordinate male. Jealous-like reactions are also prevalent in many animals under other circumstances where a desirable commodity is either being hoarded and enjoyed by another individual, and dog and cat owners frequently report behaviour akin to jealousy being displayed by their animals towards their partners.

Faces and anger

The amygdala is important for interpreting facial expressions of anger and damage to this region prevents recognition of angry faces and brain imaging studies have shown that the sight of angry faces activates it, especially in the right brain hemisphere. Brain recordings from monkeys have also shown responses to angry faces in this brain region.

Recognising anger on faces seems to be pretty universal across species since our sheep can not only recognise different human faces but consistently chose smiling or neutral expression faces rather than angry versions of the same face. I am sure many dog and cat owners would also claim that their animals can recognise an angry human face.

Sadness

Sadness, grief and depression are also powerful human emotions and in humans we know that parts of the frontal and cingulated cortices are important in controlling these. Imaging studies have also shown activation of the anterior part of the insula cortex when sad events are remembered. It seems that when the ability of some areas of the frontal cortex to reduce negative affect is impaired then we can become overwhelmed by these emotions. This is associated with reduced activity of the neurotransmitters serotonin and noradrenaline. Drugs like the selective serotonin reuptake inhibitors (SSRIs), notably fluoxetine (PROZAC), and combined selective serotonin and noradrenaline reuptake inhibitors (SNRIs such as Venlafaxine) effectively turn up the inhibitory gain in this brain region to help suppress the activation of lower brain centres controlling negative emotional responses and to increase that in centres controlling positive ones.

Animals diagnosed as suffering from depressive symptoms primarily from their behaviour also seem to improve with the same types of drugs that are effective in treating depression in humans. Once again this observation alone is persuasive that these emotions may be very similar in other species.

Can animals experience grief?

In some of my previous lectures I have made the point that there is not much evidence for many other mammals displaying either behavioural signs of grief or helping other wounded or trapped individuals. However it does happen and there are a number of examples cited in books by Masson and Bekof (referenced below). The species that are notable in this respect are the great apes, dolphins and whales and elephants. Masson and McCarthy's book is entitled "When Elephants Weep" because one of the central questions that they cover is whether when elephants produce watery discharges from their eyes they are actually crying in the same way as a human would. There are all kinds of simple physiological explanations for these discharges and so it is very difficult to make objective conclusions. However, there are many reported instances of elephants standing guard over dead companions for days and particular mothers whose offspring have died. In chimpanzees too, primatologists such as Jane Goodall have reported individuals that following the loss of a mother simply pine away and die not matter what help is given.

In social mammals emotional bonds between mothers and their offspring are extremely influential on the offspring's behaviour for the rest of its life and can reach the level of a form of social exclusivity that mother and baby become a fully independent social unit. It is not terribly surprising therefore that if this bond is broken it will evoke a profound emotional reaction.

Similar exclusive relationships between humans and their companion animals can sometimes cause the same profound emotional reactions when the human dies.

Shame and guilt

These are clearly moral emotions and many would claim that these are unique to humans. It is easy to imagine that a dog or cat that has done something they know their owners will disapprove of is exhibiting shame or guilt when they try to avoid contact with you and look as if you have just told them off severely even when you haven't. However, this may only be submissive behaviour in anticipation of an outcome that they have learned is likely to happen (being told off) as a result of their actions rather than shame or guilt.

The most convincing demonstration of another animal exhibiting shame, for example, would be where they showed clear behavioural signs of depression at failing to achieve something that another individual expected them to. When human children are put in a situation where they fail a task that an adult has told them they should be able to do then they often slump and touch their foreheads. Great apes that have been taught sign language, and so can communicate to some extent with humans, also show these same behavioural signs when they fail a task.

Joy and Love

Joy and love are emotions that are not easily interpretable in terms of being part of some biological rapid response mechanism for promoting survival. As I discussed in my last lecture the expression of many positive emotions, such as when we smile or laugh, is not only associated with making us feel good but is a useful long-term social bonding tool since such facial expression are highly contagious (i.e. “smile and the world smiles with you” is literally true and therefore makes many other people experience pleasure simply as a result of you communicating that emotion yourself). Looking at many other animal species when they are playing for example or showing pleasure during bouts of grooming it is easy to reach the same conclusion that there is a similar contagious outbreak of pleasure that is helping promote social bonds. When animals play this causes release of dopamine in the pleasure centres of the brain and grooming also seems to promote the release of endogenous opioids in the brain that may also promote pleasure.

As far as humans are concerned it is interesting that positive emotions like joy and happiness also seem to involve the frontal cortex and limbic structures although there is a tendency for the left side of the brain to be more involved than the right. It is probably far too simplistic to consider that when we are happy we are dominated by the left side of our brains and when we are unhappy the right side is in control. However there does seem to be some differentiation between these opposing states between the two brain hemispheres.

For many the inclusion of love as a primary emotion would not be considered appropriate. There are two main reasons for this. The first is that, unlike the other emotions we have considered, it does not have a distinctive facial or other behavioural expression (i.e. just by looking at someone in isolation you would find it difficult to tell that they were in love – although you might be able to do so if you viewed them interacting with their loved one). The second reason is that many anthropologists and psychologists have made the argument that love is a “drive” just like “hunger”, “thirst” and “sex” (Fisher et al, 2002). In its most extreme form, it can be so strong that it takes precedence over all else. However, many of the other emotions we have considered can be expressed at similar “drive” like intensities and equally there are many who would argue that people in love do communicate this state through physical signs – albeit subtle. Also, to omit love from a list of basic emotions would fly in the face of thousands of years of human art, poetry and literature.

As humans we are very much preoccupied with the concept and desire for “romantic” love and this would be very difficult to show in other species. Several brain imaging studies have now been carried out in humans while viewing a picture of a lover as opposed to a friend. These tend to be carried out on couples still in the initial passion of a new romance rather than in long-term partners. The patterns of activation reported have universally included brain dopaminergic pleasure centres (nucleus accumbens and ventral tegmental area) and other regions of the cortex associated with emotions (the cingulate cortex and the insula) (Bartels and Zeki, 2000). Luckily the part of the insula cortex activated is not quite the same as that associated with disgust although they are close and so love and hate may not be that far removed, at least spatially, in the brain. Most researchers consider that feelings of love for a partner are particularly generated by the release of dopamine in the brain’s reward centres.

Can other animals experience love?

If there is the equivalent to love in other animals the place to look would obviously be those species where parents bond strongly with their young and/or form long-term monogamous pair bonds. There are some very good examples of this and I have covered much of the research involved in two of my previous lectures ("Sexual conflict and the emergence of social equality and monogamy", November 2002 and "Is having a good parent more important than having good genes", December 2002).

The only two species that have been looked at in detail might seem, at first sight, the most unlikely. In the first place there is my own laboratory's work on sheep, both in the context of females being attracted sexually to males and mothers bonding exclusively with their lambs. The second area is work on monogamous vole species by a number of scientists in the USA, including Tom Insel, Larry Young (Insel and Young, 2001) and Sue Carter. The vole species (notably the Prairie vole) that bond with an individual sexual partner only do so after having had sex with them. Once the bond has been formed they remain together and if one of the partners dies the other will often not form another bond again.

The main similarity of the findings with these animals and humans is that dopaminergic pleasure centres such as the nucleus accumbens are also essential. For females, another chemical system in the brain that is also important is that which releases a small neuropeptide called oxytocin. In sheep this released in the brain when the mother gives birth and makes her exhibit maternal care and bond emotionally with her lambs. If this is prevented from happening then this does not happen and infusions of the peptide into the brain of a non-pregnant animal will cause it to mother and bond with a lamb within 30seconds (see Kendrick 2001). There has been much speculation that this peptide may also be important for triggering emotional bonds in humans and we know from work in sheep that when it is released it has the capacity to boost the release of both dopamine and noradrenaline – both of which are associated with arousal and pleasurable feelings in humans.

The work on voles has shown that males may be slightly different in that their bonds with a female sexual partner seem to depend on another closely related peptide, vasopressin – this can also modulate dopamine and noradrenaline release.

So while it may not be possible to say whether other animals can really experience feelings of love, very similar things are going on in their brains as in ours under circumstances where close social and sexual bonds are present.

General differences between humans and other animals

From the review of human and animal emotions that I have given so far I have made it clear that if animals were to "feel" emotions in the same way as us, they would have to have a similar capacity for consciousness and self-awareness and, arguably, a language based communication system. While some other animals may have some of these abilities they are clearly far less developed than our own and this would be expected given that in humans the parts of the brain neocortex dealing with these faculties have expanded dramatically in size (particularly the frontal cortex which is a very important emotion control centre).

Our enhanced capacities for consciousness, self-awareness and reflection, language and memory have also considerably expanded the time-domains in which we can exist. We are not merely creatures locked in the present but have an amazing capacity to reflect on and learn from the past and to calculate likely events even into the long-term future. Indeed, we tend to carry time around with us in our heads whereas other animals have only a limited ability to do this and are mainly responsive to moment by moment changes in their environment. This extension of our time domain has great cognitive advantages but it also enhances our capacity for suffering and paranoia and an ever-present knowledge of our mortality. Without a developed sense of self-awareness it is not possible for other animals to experience the so called "moral" emotions like shame, guilt and pride etc and I have already argued in previous lectures that there is little good evidence for self-recognition in animals other than great apes and perhaps dolphins.

While we consider ourselves to be constantly operating in conscious mode when we are awake we all know that there are times when this is not true. When you automatically drive to work on Saturday instead of to some recreational venue or you suddenly find you have walked somewhere without having intended to, or even shut off in front of the television. Operating a brain in permanent conscious mode not only requires a highly developed neocortex but this also burns up considerable energy. So you should only use conscious mode when you really need it and go onto unconscious autopilot when you don't. You can still do a large number of routine things quite effectively in unconscious mode.

My conclusions from this are that with a less developed neocortex, and only using what conscious capacity you have when it is required, must of necessity mean that many other animals probably only spend a small proportion of their waking life in full conscious mode. However, I do not ascribe to the view that they are all incapable of consciousness at all since many have sufficient neocortical development and sophisticated cognitive and social skills to make such a conclusion untenable in my opinion. Nevertheless, a limited capacity for consciousness translates into a similar limited capacity for experiencing "feelings" associated with emotional states.

Perhaps it will be useful to end by simply trying to give a practical example of what I mean by this. Let us consider for a moment a human and a dog that are very close to one another but have been separated for several months.

What the human may think and feel during a period of separation from a pet dog

The human has the capacity to "think" about their missing canine friend every waking moment (and even during sleep which will be a subject of a further lecture next year). Those thoughts could take all sorts of different forms ranging from remembering specific occasions and activities where they were together over the years to what they might do the moment when they meet again and what they might do in the future. External experiences will also trigger thoughts about the absent dog (i.e. seeing other dogs being taken for a walk, or pictures of dogs in shops or peoples houses or on the television and so no). The human could also start to imagine all kinds of scenarios whereby the dog might be injured or die or be stolen in their absence and that they might never see them again. If other things are not going well in their life they may have a reduced ability to suppress such negative and fatalistic emotions. Added together this could lead to the human experiencing emotional distress at the separation at varying levels for the whole period of separation. When the human is finally re-united with the dog he will, of course, have no problem recognising him and will experience intense positive emotions of joy probably tinged with relief. He will also show typical behavioural signs of excitement and joy and pat or hug the dog or indulge in a spot of play-fighting and offer lots of vocal encouragement. If the intensity of his emotional distress during the separation was indeed both high and constant he may even be totally exhausted by the experience.

What the dog may think and feel during a period of separation from a human

Like the human the dog will have the capacity to remember their human owner for a considerable period of time and the stronger the emotional bond between them has been the longer such a memory is likely to persist. However, the dog is more restricted to experiencing life in response to moment by moment events. As such the various things that they normally do or are exposed to at different times during the day will have the potential to trigger the memories of their absent owner and their past activities together, and to experience distress. While such reactions may continue over some period of time (especially in the early period of separation) the dog has far less potential for introspective reflection on possible outcomes of the separation (i.e. he is unlikely to reflect on the possibility that the owner might be injured or die or be abducted for example) or planning what they might do together when re-united. The upshot of this is that the dog is unlikely to experience prolonged feelings of distress at being separated from its owner for the whole period of that separation or to consider a host of "what if" scenarios which could intensify that distress.

It is possible however that the dog may remain physiologically in an emotional state of distress even though it might only feel the consequences of this sporadically. Like the human alexithymic this might result in him performing inappropriate actions such as excessive grooming or trashing the joint in order to relieve the pressure cooker of his negative emotional state (the human who can normally interpret the cause of his emotional state through his more enduring experience of conscious feelings should, in most cases, be able to defuse the situation by thought rather than action).

When the dog is re-united with their owner then recognition will also be instant since and again, like the human, they will exhibit behavioural signs of excitement and joy at the re-union (barking, jumping up, tail-wagging etc). He may also experience limited conscious feelings of pleasure.

Given growing evidence that animals like dogs and cats are able to sense that their owners are returning long before they actually arrive it is possible that the dog may have been showing behavioural signs of anticipating its owner's arrival considerably in advance of the event.

Final thoughts

The fact that humans are able to conjure up a host of different emotions by simply imagining what might happen under a variety of different circumstances is both a great advantage in terms of strategic planning and a disadvantage when the individual is unable to control, such thoughts as in depression and paranoia. As Shakespeare so aptly puts it:

"Is it not monstrous that this player here,

But in a fiction, in a dream of passion,

Could force his soul so to his own conceit,

That, from her working, all his visage wann'd;

Tears in his eyes, distraction in's aspect,

A broken voice, and his whole function suiting

With forms to his conceit? And all for nothing!"

- (Shakespeare – Hamlet, Act 2 Scene 2)

I won't rule out the possibility that other animals can't mimic emotional states that they are not experiencing but for the most part one of the advantages we have in our associations with them is that we assume they cannot lie to us. This assumption can clearly not be made with the same degree of confidence when dealing with other humans.

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Selected references

Bartels A and Zeki S (2000) The neural basis of romantic love. NeuroReport 11:1-6.

Becerra L, Breiter HC, Wise R, Gonzalez RG, Borsook D. Activation of Reward Circuitry following Noxious Thermal Stimuli. Neuron 2001; 32: 927-946.

Bekoff M (2000) The Smile of a Dolphin: Remarkable Accounts of Animal Emotions. Discovery Books.

Bekoff M (2002) Minding Animals: Awareness, Emotions and Heart. Oxford University Press.

Calder AJ et al (2000) Impaired recognition and experience of disgust following brain injury. Nature

Damasio A (2003) Looking for Spinoza: Joy, Sorrow and the Feeling Brain, Harcourt (available from Amazon)

Darwin C (1872) The Expression of the Emotions in Man and Animals. John Murray, London.

Fisher HE et al (2002) Defining brain systems of lust, romantic attraction and attachment. Archives of Sexual Behavior 31:413-419.

Insel TR and Young LJ (2001) The neurobiology of attachment. Nature Neuroscience Reviews 2: 1-8.

Kano M et al (2003) Specific brain processing of facial expressions in people with alexithymia: an H 2 15O-PET study. Brain 126:1474-1484.

Kendrick KM (2000) Oxytocin, motherhood and bonding. Experimental Physiology 85S 111S-124S.

Le Doux (1996) The Emotional Brain: The Mysterious Underpinnings of Emotional Life.

Le Doux J (2002) Synaptic self: How Our Brains Become Who We Are. MacMillan, London

Luan Phan K, Wager T, Taylor SF and Liberazon I (2002) Functional neuroanatomy of emotion: a meta-analysis of emotion activation studies in PET and fMRI. NeuroImage 16:331-348.

Masson J and McCarthy S (1994) When Elephants Weep. The Emotional Lives of Animals. Vintage, London (available through Amazon)

Plutchik R (1980) Emotion: A Psychoevolutionary Synthesis, New York, Harper and Row.

Small DM et al (2001) Changes in brain activity related to eating chocolate. Brain 124:1720-1733.