Quality of life and the evolution of the brain

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Abstract

The dual problem of explaining brain evolution and the way in which it has led to wide species differences in behaviour and physiology has often appeared intractable to scientists. The main limiting factor is that we do not understand enough about how brains work to appreciate why gross or fine morphological differences can lead to the considerable across- as well as within-species differences in behaviour. Even at a molecular level, while two-thirds of our genes are involved in regulating brain function, there is a high degree of homology within different phyla. In the context of quality of life (QoL), arguably the most important consideration is that the brain you have evolved is adapted to the environment you are living in and is capable of generating 'conscious' experience. When that environment is radically altered, issues arise regarding whether there is sufficient adaptability to cope and the extent to which mental as well as physical suffering might be experienced as a consequence. At the other end of the spectrum there is the question of how enriched social and physical environments might enhance QoL through promoting positive affect. Here I will discuss potential functional contributions of differences in brain size and organisation and the impact of experience. I will mainly focus on mental functioning and show particularly that capacities for consciousness, emotional experience, social interaction and cognition and behavioural flexibility are likely to be widespread in other animal species, even if less developed than in humans.

Keywords: animal welfare, brain evolution, cognition, consciousness, emotion, quality of life

Where have the major changes occurred in the brain during evolution?

Traditionally, brains have been considered to have three major subdivisions: the hindbrain, the midbrain and the forebrain. These all interact and are each essential for an organism's normal function and survival. However, the basic organisation and structure of the brainstem and the midbrain has not altered much from reptiles through to humans. These two subdivisions deal with important evolutionarily conserved functions, such as homeostatic regulation of many bodily functions, general arousal and sleep, and provide an essential modulation and control of the forebrain that regulates all other aspects of behaviour, including cognitive, motivational and emotional ones, as well as other key aspects of physiological functioning, such as reproduction and stress responses.

The forebrain also has extensive regions that have apparently altered relatively little during the course of brain evolution, including those in the limbic system and hypothalamus which are important for the control of highly motivated behaviours (ie hunger, thirst and sex), hormonal regulation via the pituitary gland, and basic emotional responses, such as fear, which are controlled by regions such as the amygdala. What has changed considerably during the course of brain evolution is the brain's 'top-down' rather than 'bottom-up' control centres — namely, the size and complexity of the neocortex, which forms dense layers of cells and fibres over the structures controlling basic functions essential for the execution of routine behaviours that promote both survival and reproduction.

The mammalian neocortex is considered to be the part of the brain that deals particularly with many of its higher functions such as cognition, consciousness, language, moral judgements and more complex emotions, self-awareness, and theory of mind. In particular, its development is seen as an essential process in developing a more flexible control over even the most basic behavioural functions that in many species with either no neocortex, or a poorly developed one, are rigidly controlled by the direct actions of hormones or sensory stimuli which evoke standard, almost reflex types of responses to stimuli in the environment, and exhibit only limited flexibility (see Keverne 2004).

The question of whether species with the most developed neocortices have simply expanded size and synaptic complexity or have also evolved different macrostructural or microstructural features that are of functional importance is still an open one. In terms of macrostructural changes, the large increase of size in the frontal cortex of primates and notably humans has received the most attention. As we will see during the course of this review, the frontal cortex

figures prominently in almost all cognitive and emotional behaviours and is important for the most complex of these, such as moral judgements and theory of mind. In humans this is the slowest maturing brain region (up to the end of our second decade) and it needs to assimilate and integrate all major aspects of cognitive and emotional experience.

Language areas in the human brain are also often regarded as examples of macrostructural differences between human and other brains, although Broca's area has been identified in the chimpanzee brain (Cantalupo & Hopkins 2001), and it seems that this and other language regions in the left brain hemisphere have been taken over for this role and expanded in size.

In terms of microstructural differences, hominids and great apes have so called 'spindle' cells in layer V of the neocortex (anterior cingulate and frontoinsular cortices), which are not found in other species (Nimchinsky *et al* 1999). These cells appear to provide a possible integrating role with other parts of the cortex and with subcortical structures involved with higher social and cognitive functions, such as theory of mind and social recognition, communication and cooperation as well as emotions. At this point, however, we do not know for sure what the key functions of these spindle cells are and whether they really do represent an important index of higher social and intellectual functioning. Interestingly, it has recently been found that the neocortex of the humpback whale also contains these spindle cells in layer V (Hof & van der Gucht 2007). Since cetaceans diverged from terrestrial mammals 50–60 million years ago it would seem that this is likely to be a case of parallel evolution. However, other cetaceans, such as dolphins, do not possess these cells and yet are widely regarded as being highly social and intelligent. Clearly it would be of great interest to discover if the mental capacities of humpback whales are indeed more sophisticated than those of dolphins.

Another way in which microstructural organisational changes may have contributed to altered brain function is what has been termed 'molecular evolution'. This proposes that although two-thirds of genes are expressed in brain cells and there is a very high degree of genetic homology across species, it is possible that genes associated with one function in a particular species might have become adapted to subserve another function in others. An example of this that has been proposed is the *foxP2* gene, which is thought to play a critical role in language production in humans but also plays a role in song production and vocal learning in birds and other mammals. The protein associated with this gene in humans has undergone a few amino acid substitutions, although whether this has contributed specifically to the development of human language is difficult to assess (see Scharff & Haesler 2005; Webb & Zhang 2005). It remains an interesting possibility that altered genetic contributions to organisational aspects of brain function could help to explain how, even with apparently similar gross brain morphology, considerable differences in behavioural complexity can occur.

Evolutionary pressures associated with increased brain size

Many attempts have been made to correlate brain size with key behavioural requirements in different species. These have not always been very successful, and naturally it is somewhat naïve to simply equate functional sophistication with the actual size of something so complex in its organisation as a brain. Nevertheless, positive correlations have been found with factors such as behavioural flexibility and social group size and social intelligence (Reader & Laland 2002). This makes a good deal of sense because species that, for example, are demonstrably less dependent upon hormonal changes to regulate sexual and parental behaviours, and are capable of exhibiting more sophisticated aspects of social cognition, do tend to have more extensive neocortical development. Old World monkeys and the great apes are obvious examples of this.

Naturally, much of the focus in the brain size debate has been on the difference between humans and other species, and even between modern humans and our hominid ancestors. Certainly the huge difference in the cognitive and emotional capabilities of humans, compared with other species, is difficult to explain purely in terms of increased neocortical size even though a human brain is three times larger, for example, than that of a chimpanzee. This has led to proposals that organisational differences, particularly those associated with the evolution of language production and processing, are also of great importance. What is important in the context of this paper, however, is that human brain evolution has been subject to the same evolutionary pressures as for other species and that undoubtedly behavioural flexibility and the need to live and interact within larger social groupings in order to survive have also acted to shape the development of the human brain.

It is also important to point out that brains may have evolved different strategies to come up with the same solution. How does one compare the neocortex of a mammal with the cortex of a bird? They have basic similarities, of course, but they are also very different in the way they are structured and organised. The key observation is that they can both provide the same additional functions and flexibility, particularly in the cognitive domain. Even within the mammalian phyla, the organisation of the neocortex can vary markedly across species. Marine mammals in particular seem to have a slightly different organisation to terrestrial ones. Dolphins, for example, do not seem to have a pronounced frontal cortex and yet this is one of the key brain regions which has increased in size during primate evolution and is considered to have led to increased cognitive and emotional capacities in these species, and particularly in humans.

Quality of life considerations

Other papers will consider in more detail the precise definitions and measurement of quality of life (QoL), whereas I will focus on discussing key mental processes which make QoL a relevant issue when considering any species, and I

will confine myself to the simple assumption that, for any individual of any species, good QoL will arise primarily from being able to cope with its environment where it will experience 'good' feelings and a few 'bad' ones. I will say from the outset, however, that we are yet to achieve sufficient understanding of how brains function to be able to use brain metrics or activity measurements in some form of objective assessment of precisely what another animal can think or feel. However, the increasing understanding of how the human brain functions under different circumstances, and the demonstration that key aspects of cognitive and emotional behaviours in other species involve similar brain organisation, will act to further promote consideration of issues concerning other species' QoL.

Capacity for consciousness

Proof of the capacity for conscious perception and experience lies at the heart of any consideration of whether QoL issues apply to another being. In the absence of consciousness, capacity for either suffering or joy becomes irrelevant and any concerns would then represent unjustifiable anthropomorphism on the part of a human observer capable of consciousness and emotional experience.

So, are the brains of other animal species capable of supporting consciousness? This has been the subject of considerable debate by scientists, theologians and philosophers alike. While we lack any clear understanding of what makes the human brain capable of consciousness — other than, it seems, a functional neocortex — it is quite easy to find proposals supporting diametrically opposed viewpoints, because there is no definitive empirical way of answering the question. Much is made of the fact that even quite complex behaviours can be carried out by mindless computer-based machines, and so why might that not be the case for animals with simpler brains than our own? Similarly, we all know that brains carry out a vast array of important maintenance and routine functions of which we are unconscious. For some almost automatic basic motor skills, such as walking, trying to perform them 'consciously' can be extremely difficult. There are also cases of 'blindsight' in humans, where damage to visual centres in the brain can result in individuals saying that they are not aware of seeing objects in their environment but who nevertheless show evidence that their brains can process and act upon information from these objects.

Comparing brains with computers is an irrelevance, however; they do not function in the same way at all. Most biologists are prepared to support the general concepts of Darwinian evolution. Thus, while traits that promote survival are selected for and refined, it is generally expected that some version of them will be present in other species too (ie the concept that a unique trait could evolve within a single species where it involves biological processes common to many other different species is difficult to support). So, for many, to say that consciousness spontaneously developed in the human brain because of, for example, a side-effect of positive selection for increased size, seems unlikely. Rather, what is more likely is that consciousness is a trait that has evolved in the brains of many species and that in humans it has been selected for strongly in parallel with the need for bigger brains in order to develop more sophisticated and flexible behavioural and social repertoires and skills which promote survival (a case of 'co-evolution', if you like).

So, are there some accepted components of brain evolution which might distinguish brains that are capable of consciousness from those that are not? While all major brain subdivisions clearly play important roles in regulating consciousness, it is generally accepted in humans that a functioning neocortex is a key requirement. Thus, while humans without a functional neocortex can survive, they do not appear to exhibit a capacity for consciousness. This leads to the possibility that species without a neocortex, such as amphibians and fish, may not be capable of any form of consciousness, in which case QoL issues would be of little relevance since they could not experience 'feelings'. At present there is no easy way to test for this possibility, although returning to Darwinian principles one has to entertain the possibility that brains may have evolved other ways of supporting consciousness even without a neocortex. The neocortex might perhaps have taken over this function from other more primitive structures, for example.

A second consideration is the requirement for sleep. This is a biological need for a wide range of species and certainly for birds and mammals. We still do not know what all the benefits of sleep may be, but there is no doubt that we and other mammals cannot survive without it. What is certain is that it is fundamentally an unconscious state and, even in the case of paradoxical or rapid eye movement sleep, distinct from a conscious waking state. One obvious potential purpose for sleep is to give the brain a break from operating in a metabolically demanding 'conscious' mode. If so, that immediately admits the conclusion that all animals which need to sleep must have some capacity for consciousness when they are awake. Looking at it from another perspective, and leaving aside the obvious metabolic argument, maintaining a conscious state during long hours of enforced inactivity during each day (ie during the hours of darkness for diurnal species) could be psychologically very stressful and impair survival skills during the active parts of the day.

We are now beginning to understand something about the neurobiological correlates of consciousness in humans. One approach, therefore, to being able to establish a capacity for consciousness in another animal species is to show that its brain exhibits similar activity patterns to those found in the human brain during conscious experience. This is not definitive proof, of course, but it does provide supportive evidence and raises the obvious question of how a human brain utilising a specific set of brain structures could generate consciousness whereas the same set of structures in another animal species could not.

Some of the most revealing experiments studying how the emergence of consciousness is organised within the human brain are those which have focussed on primary needs such

as thirst and hunger for air. These are important survival imperatives for any species. Human brain imaging studies have found a strong correlation between activation of parts of the cingulate cortex and the reported emergence of consciousness of being thirsty (Denton *et al* 1999) or breathless (Liotti *et al* 2001) following experimental treatments that can induce these states. Although no studies of this kind have yet been carried out in other animal species, the cingulate cortex is well developed in all mammals, and studies that we have carried out in sheep, for example, have revealed that this structure is strongly activated under many different circumstances where perception of important social stimuli is involved (Broad *et al* 2000; da Costa *et al* 2004).

Similarly, we know that when humans are asked to form visual mental images of faces, this activates many of the same brain regions as does actual perception of faces (Kanwisher *et al* 1996). Our evidence from studies on sheep using non-visual cues that could be anticipated to evoke a visual mental image of an individual's face suggests that the same pattern of activation is also occurring as with actual perception of a face (Kendrick *et al* 2001b; Tate *et al* 2006). Neural circuits that show selective electrical activity changes in response to the actual appearance of faces can also respond when they are not visible; for example, in anticipation of an individual appearing, or after they have disappeared.

Capacity to experience emotions

The parts of the brain controlling basic emotional responses such as fear, anxiety and anger are relatively well understood and are primarily subcortical and highly conserved across evolution from reptiles through to mammals (LeDoux 2003). These emotional responses all subserve important survival functions and particularly 'fight or flight' responses. Much less is known about positive emotions, although these are clearly of great importance in the context of QoL considerations because improvements in the latter must involve promoting positive emotions as well as reducing negative ones. Brain control over the expression of positive emotions intrinsically involves both dopaminergic and opioid systems, which are again localised in subcortical and highly evolutionarily conserved brain regions (Burgdorf & Panksepp 2006).

The experience of 'conscious feelings' and the ability to interpret and control emotional responses is heavily dependent upon interactions between subcortical regions and the neocortex. Although we do not fully understand how the human brain allows the experience of feelings, any more than consciousness, again it seems unlikely that only the human brain has evolved the necessary organisational connections between subcortical regions and the neocortex to allow this experience. Nevertheless it is important to point out that behavioural responses to emotive stimuli do not necessarily result from the experience of feelings for humans any more than for other species. For example, brain circuitry controlling fear responses has a fast-track totally subcortical route that enables an automatic rapid flight response. In this respect it is possible to say that you do not run from a threatening object because you feel fear, but rather that you feel fear because you are running from it — in other words, the feeling can be a consequence rather than the cause of an emotional response. This has led many neuroscientists to propose that other species might not need to experience feelings at all even though they can display complex emotional responses (in just the same way as complex behaviours can be performed without invoking a capacity for consciousness). Again, therefore, this could lead to the conclusion that QoL considerations are not of serious relevance for other species.

An obvious prediction is that if animals are experiencing feelings in emotional situations then the brain neocortex should be active, particularly in those regions involved with emotional control. From my own research it can be seen that when an animal such as a sheep experiences separation anxiety and shows behavioural, hormonal, autonomic and brain indices of fear and anxiety, alleviating these symptoms by showing them pictures of a familiar face is associated with considerable neocortical activity. This activity is particularly localised in regions such as the frontal and cingulate cortices involved with consciousness and emotional control (da Costa *et al* 2004). Similarly, if we look at the patterns of brain activity that occur in humans viewing face pictures of a romantic partner or their infant (Bartels & Zeki 2004; Aron *et al* 2005), they are not fundamentally different from those seen in a female sheep seeing an attractive male or its lamb (da Costa *et al* 1997; Fabre-Nys *et al* 1997; Ohkura *et al* 1997). Subcortical dopaminergic brain reward centres are activated, as well as areas of the neocortex involved in emotional control. However, an important difference is that these patterns of activity only occur in sheep following appropriate sex hormone priming, whereas in humans they are clearly relatively independent of such priming. This shows that top-down control from the neocortex to subcortical structures in humans has evolved to be more influential than the bottom-up hormonal control that is characteristic of the majority of species with a less developed neocortex.

Capacity to learn and remember

Again, as with consciousness and emotional experience, the neocortex is clearly important for learning and memory and particularly for aspects of rule following and dealing with abstract concepts. However, subcortical structures such as the hippocampus are once again critical for most forms of new learning and this region is also highly conserved across species. Emotional learning involving another conserved subcortical structure, the amygdala, is also very efficient in a wide variety of species.

Brain mechanisms subserving learning and memory have naturally evolved to deal with species-specific adaptations to their environment. It therefore makes little sense to ask the question if one species is more intelligent than another, because performance will be highly task- and environment-dependent. What a large neocortex gives is greater flexibility of learning, increased capacity to integrate different information and more extensive potential for conscious planning.

When it comes to learning about things that are important for the survival of any species, it quickly becomes clear that the speed and duration of learning are remarkable. This includes learning to recognise new foods and avoid toxic ones, learning where to go to find food or shelter, avoiding dangerous places, and identifying important conspecifics and their emotional signals. Thus, learning to identify novel palatable or unpalatable foods will generally take only a single trial, and a mouse, for example, will remember the smell of another individual for a week or more after an encounter lasting only a few minutes. Similarly, social transfer of food preferences and some imitation behaviours can also be very rapid and long-lasting, and food-storing animals can remember dozens of different locations where they have buried caches.

One of the key advantages of a larger neocortex is being able to hold information in consciousness for long periods of time. This is essential for complex planning. For many non-primate mammals, tasks requiring information to be held in working memory for more than around 10 seconds are very challenging, whereas for humans they are relatively easy.

Ability to adapt as a result of life experiences

This is also of great survival value and is particularly evident in the context of early experiences of emotional bonds. Rat pups raised, for example, by attentive mothers which exhibit high levels of licking and grooming show a reduced stress reaction and good spatial learning and also become attentive mothers. On the other hand, pups raised by mothers with low levels of licking and grooming show an enhanced stress response and poorer learning and are also less attentive mothers. Cross-fostering and molecular genetic studies have revealed that this is caused by the pups' experience of these different types of mother provoking epigenetic changes that influence brain function (Meaney & Szyf 2005). The brain structures involved in this are once again primarily subcortical.

Similarly there is strong evidence from the work of my own laboratory on sheep and goats that the maternal bond influences the physical characteristics (ie appearance) that offspring find socially and sexually attractive in other individuals (Kendrick *et al* 1998; 2001). This type of 'sexual imprinting', which was originally discovered in birds, also seems to play some role in humans as well (Perrett *et al* 2002; Little *et al* 2003; Bereczkei 2004).

The mechanisms whereby experience of parental bonds can influence these, and many other, preference behaviours (both appetitive and aversive) are not completely understood. However, it is likely that there is an important role for several neuropeptides that promote the formation of social, filial and pair bonds — notably oxytocin and vasopressin (Kendrick 2001; Hammock & Young 2006). These not only interact with dopaminergic brain reward systems but also may facilitate changes between these systems and sensory social recognition regions of the brain, such that a particular individual, or types of physical features, elicit the maximum pleasurable response. Once again these mechanisms appear to be acting primarily at subcortical levels but allow even

species with a less developed neocortex to undergo quite radical adaptations in their behaviour that are not genetically 'hardwired' but are the result of experience.

From a QoL perspective, the most important conclusion is that early emotional experiences in the context of social bonds can have profound influences on the lifelong 'likes' and 'dislikes' of an individual animal because the brain has evolved this particular adaptation. Thus, the quality of an individual's early social and physical environment may well permanently influence its potential to experience a positive QoL no matter how it is treated subsequently.

Having a concept of time

Time is an important frame of reference for storing and using information. Knowing 'when' something happened, as well as 'what' it was and 'where', potentially allows an individual to consider past and future as well as present. This is known as episodic memory and has been difficult to demonstrate in other species (Suddendorf & Busby 2003), although notable exceptions are food-storing birds, such as scrub jays, which show good behavioural evidence that they can use time information to inform them for how long a particular food has been buried (Clayton *et al* 2003).

While conserved subcortical regions (eg suprachiasmatic nucleus) are important for regulating activity, physiological and biochemical rhythms, time perception involving durations of many seconds or longer involves frontal and parietal regions of the neocortex, reflecting a greater consciousness component. The ability to travel mentally back or forward in time to predict likely events in the future has a separate representation in the human brain from other kinds of memory and even self-awareness, although like self-awareness it involves regions of the frontal cortex (Okuda *et al* 2003). Humans who have suffered damage to this region have impaired ability to carry out any form of mental time travel to recall past events or predict future ones other than for very short periods (literally a few minutes). These individuals report that when they attempt to travel more distantly into the past or future their minds go completely blank.

Once again, therefore, it is the evolution of a larger and more complex frontal cortex seen in humans and other primates that has allowed a greater capacity to consider future and past events and actions. How this occurs in avian species is unknown, although it is probably also primarily cortical. Clearly, QoL considerations for individuals from species which can conceptualise that their present conditions and feelings are better or worse than those that have occurred in the past, or that might occur in the future, are greater than in those species with limited capacity to do this.

Being aware of self and what others are thinking and feeling

In 1970 Gordon Gallup Jr published a landmark paper (Gallup 1970) which has been the subject of controversy and debate ever since. He reasoned that if animals could recognise their image in a mirror as a representation of themselves rather than of another individual, then they must

have self-awareness in the sense that they could become 'the object of their own attention'. Since this original study, 73 out of 163 chimpanzees have been shown to pass the mirror test, 5 out of 6 orang-utans but only 6 out of 23 gorillas. Dolphins also seem to be able to recognise their images (Reiss & Marino 2001) and most recently an Asian elephant (Plotnik *et al* 2006). However, other animal species tested show no convincing evidence that they can do this and treat their image in the mirror as if it were another animal. Humans develop this form of self-recognition from around 18–24 months of age.

A central question arising from this kind of evidence for self-recognition is whether it is also good evidence that individuals of a particular species are able to attribute and predict mental states in others — so called 'theory of mind' — and empathise with them. Such capacities would clearly have a major impact on QoL issues. This is a difficult problem to tackle experimentally but there is little doubt that a number of animal species, particularly the great apes, show evidence of cooperation and also deception. Nevertheless, even the chimpanzee's experimental findings still call into question whether they can conceive of others and empathise in a manner similar to ourselves (Povinelli *et al* 2000).

The discovery of cells in premotor and parietal cortices of monkeys that become active not just when an animal performs an action but also when it sees others performing the same action has provided a potential neural correlate for imitation and empathy (Iacoboni & Dapretto 2006). These have been called 'mirror' neurons and in humans it has been suggested that they may become dysfunctional in conditions such as autism. In humans also, the network of these neurons in the frontal and parietal cortices is activated during self-face recognition (Uddin *et al* 2005). The extent to which these types of 'mirror' networks exist in other species has yet to be established although they are clearly present in primates. It seems likely that they are present in other mammals too, given the fact that imitative behaviour is exhibited by a variety of species. Interestingly, one of the primary language areas in the human brain, Broca's area, is also involved in action understanding and imitation (Nishitani *et al* 2005).

Neuropsychological studies on humans with brain damage and functional brain imaging techniques have also now given us a good idea of the critical brain regions for self-recognition and an associated human theory of mind. These studies have repeatedly emphasised a key role for the frontal cortex (Keenan *et al* 2000; Stuss *et al* 2001) and, more recently, the amygdala (Stone *et al* 2003). In both humans and other animals, damage to these brain regions is often also associated with anti-social behaviours such as impulsivity and/or aggression and poor interpersonal skills.

Overall conclusions

There is still much that we need to understand about how the brain controls cognitive and emotional behaviours in humans, let alone other species. However, what I hope this brief review of brain evolution has done is to confirm that many key aspects of consciousness, emotion and learning are strongly conserved across a large number of animal species even if they are at their most sophisticated in primates, and particularly in humans. The extensive similarities that exist between the human brain and that of other animal species makes it clear that QoL issues are highly relevant when considering a wide range of species but that the evolution of the neocortex, and particularly the frontal cortex, has significantly increased mental capacities for joy and also for suffering. While behavioural assessments will continue to provide the most important information about an individual animal's well-being, this will, I hope, be increasingly informed by what we know about the way its brain has evolved and functions in comparison with our own. This will help us both to avoid some of the pitfalls of anthropomorphism and to better appreciate what an individual animal needs and is actually capable of experiencing.

Acknowledgements

References

Aron A, Fisher H, Mashek DJ, Strong G, Li HF and Brown LL 2005 Reward, motivation, and emotion systems associated with early stage intense romantic love. *Journal of Neurophysiology 94*: 327-337

Bartels A and Zeki S 2004 The neural correlates of maternal and romantic love. *NeuroImage 21*: 1155-1166

Bereczkei T, Gyuris P and Weisfeld GE 2004 Sexual imprinting in human mate choice. *Proceedings of the Royal Society of London, Series B — Biological Sciences 271*: 1129-1134

Broad KD, Mimmack ML and Kendrick KM 2000 Is right hemisphere specialization for face discrimination specific to humans? *European Journal of Neuroscience 12*: 731-741

Burgdorf J and Panksepp J 2006 The neurobiology of positive emotions. *Neuroscience and Biobehavioural Reviews 30*: 173-187

Cantalupo CC and Hopkins WD 2001 Asymmetric Broca's area in great apes. *Nature 414*: 5

Clayton NS, Bussey TJ and Dickinson A 2003 Can animals recall the past and plan for the future. *Nature Reviews Neuroscience 4*: 685-691

Da Costa APC, Broad KD and Kendrick KM 1997 Olfactory memory and maternal behaviour-induced changes in *c-fos* and *zif-268* mRNA expression in the sheep brain. *Molecular Brain Research 46*: 63-76

Da Costa AP, Leigh AE, Man M-S and Kendrick KM 2004 Face pictures reduce behavioural, autonomic, endocrine and neural indices of stress and fear in sheep. *Proceedings of the Royal Society of London, Series B – Biological Sciences 271*: 2077-2084

Denton DA, Shade R, Zamarippa F, Egan G, Blair-West J, McKinley M and Fox P 1999 The correlation of regional cerebral blood flow (rCBF) and change of plasma sodium concentration during the genesis and satiation of thirst. *Proceedings of the National Academy of Sciences USA 96*: 2532-2537

Fabre-Nys C, Ohkura S and Kendrick KM 1997 Male faces and odours evoke differential patterns of neurochemical release in the mediobasal hypothalamus of the ewe during oestrus: an insight into sexual motivation. *European Journal of Neuroscience 9*: 1666-1677

Gallup GG 1970 Chimpanzees: self-recognition. *Science 167*: 86-87

Hammock EAD and Young LJ 2006 Oxytocin, vasopressin and autism: implications for autism. *Philosophical Transactions of the Royal Society of London, Series B — Biological Sciences 361*: 2187-2198

Hof PR and van der Gucht E 2007 Structure of the cerebral cortex of the humpback whale, *Megaptera novaeangliae* (Cetacea, Mysticeti, Balaenopteridae). *Anatomical Record 290*: 1-31

Iacoboni M and Dapretto M 2006 The mirror neuron system and the consequence of its dysfunction. *Nature Reviews Neuroscience 7*: 942-951

Kanwisher N, Chun MM, McDermott J and Ledden PJ 1996 Functional imaging of human visual recognition. *Cognitive Brain Research 5*: 55-67

Keenan JP, Wheeler MA, Gallup GG and Pascual-Leone A 2000 Self-recognition and the right prefrontal cortex. *Trends in Cognitive Sciences 4*: 338-344

Kendrick KM 2001 Oxytocin, motherhood and bonding. *Experimental Physiology 85*: S111-S124

Kendrick KM, Broad KD, Hinton MR, Houpt M and Skinner J 2001a Sex differences in the influence of mothers on the sociosexual preferences of their offspring. *Hormones and Behavior 40*: 322-338

Kendrick KM, Hinton MR, Atkins K, Haupt MA and Skinner JD 1998 Mothers determine sexual preferences. *Nature 395*: 229-230

Kendrick KM, Leigh A and Peirce J 2001b Behavioural and neural correlates of mental imagery in sheep using face recognition paradigms. *Animal Welfare 10*: S89-S101

Keverne EB 2004 Understanding well-being in the evolutionary context of brain development. *Philosophical Transactions of the Royal Society of London, Series B — Biological Sciences 359*: 1349-1358

LeDoux J 2003 The emotional brain, fear, and the amygdala. *Cellular and Molecular Neurobiology 23*: 727-738

Liotti M, Brannan S, Egan G, Shade R, Madden L, Abplanalp B, Robillard R, Lancaster J, Zamarripa FE, Fox PT and Denton D 2001 Brain responses associated with consciousness of breathlessness (air hunger). *Proceedings of the National Academy of Sciences USA 98*: 2035-2040

Little AC, Penton-Voak IS, Burt DM and Perrett DI 2003 Investigating an imprinting-like phenomenon in humans. Partners and opposite-sex parents have similar hair and eye colour. *Evolution and Human Behavior 24*: 43-51

Meaney MJ and Szyf M 2005 Maternal care as a model of experience dependent chromatin plasticity. *Trends in Neurosciences 28*: 456-463

Nimchinsky EA, Gilissen E, Allman JM, Perl DP, Erwin JM and Hof PR 1999 A neuronal morphologic type unique to humans and great apes. *Proceedings of the National Academy of Sciences USA 96*: 5268-5273

Nishitani N, Schurmann M, Amunts K and Hari R 2005 Broca's region: from action to language. *Physiology 20*: 60-69

Ohkura S, Fabre-Nys C, Broad KD and Kendrick KM 1997 Sex hormones enhance the impact of male sensory cues on both primary and association cortical components of visual and olfactory processing pathways as well as limbic and hypothalamic regions in female sheep. *Neuroscience 80*: 285-297

Okuda J, Fujii T, Ohtake H, Tsukiura T, Tanji K, Suzuki K, Kawashima R, Fukuda H, Itoh M and Yamadori A 2003 Thinking of the future and past: the roles of the frontal pole and the medial temporal lobes. *NeuroImage 19*: 1369-1380

Perrett DI, Penton-Voak IS, Little AC, Tiddeman BP, Burt DM, Schmidt N, Oxley R, Kinloch N and Barrett L 2002 Facial attractiveness judgements reflect learning of parental age characteristics. *Proceedings of the Royal Society of London, Series B — Biological Sciences 269*: 873-880

Plotnik JM, de Waal FBM and Reiss D 2006 Self-recognition in an Asian elephant. *Proceedings of the National Academy of Sciences USA 103*: 17053-17057

Povinelli DJ, Bering JM and Giambrone S 2000 Toward a science of other minds. *Cognitive Science 24*: 509-541

Reader SM and Laland KN 2002 Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences USA 99*: 4436-4441

Reiss D and Marino L 2001 Mirror self-recognition in the bottlenose dolphin: a case of cognitive convergence. *Proceedings of the National Academy of Sciences USA 98*: 5937-5942

Scharff C and Haesler S 2005 An evolutionary perspective on FoxP2: strictly for the birds? *Current Opinion in Neurobiology 15*: 694-703

Stone VE, Baron-Cohen S, Calder AJ, Keane J and Young A 2003 Acquired theory of mind impairments in individuals with bilateral amygdala lesions. *Neuropsychologia 41*: 209-220

Stuss DT, Gallup GG and Alexander MP 2001 The frontal lobes are necessary for 'theory of mind'. *Brain 124*: 279-286

Suddendorf T and Busby J 2003 Mental time travel in animals. *Trends in Cognitive Sciences 7*: 391-396

Tate AJ, Fischer H, Leigh AE and Kendrick KM 2006 Behavioural and neurophysiological evidence for face identity and face emotion processing in animals. *Philosophical Transactions of the Royal Society of London, Series B — Biological Sciences 361*: 2155-2172

Uddin LQ, Kaplan JT, Molnar-Szakacs I, Zaidel E and Iacobini M 2005 Self-face recognition activates a frontoparietal "mirror" network in the right hemisphere: an event related fMRI study. *NeuroImage 25*: 926-935

Webb DM and Zhang J 2005 FoxP2 in song-learning birds and vocal-learning. *Journal of Heredity 96*: 212-216