Introduction. The neurobiology of social recognition, attraction and bonding

Providing an understanding of the neural, humoral and genetic factors that control social recognition and attraction, communication and interpretation of emotional state and the formation of long-term emotional bonds is of key importance for human mental health and well-being. However, unlocking the secrets of these different aspects of the social brain presents a significant challenge to Neuroscience, since a broad spectrum of different behaviours and brain systems are involved together with a multitude of complex interactions between them. The question also arises as to whether true insights into the workings of the human social brain can be gained from detailed studies of other mammalian species that have evolved a variety of different social systems.

Advances in human brain imaging have provided us with far more detailed information about both social and emotional recognition pathways in the brain. We also are beginning to understand the substrates involved in romantic attraction and social bonds. Comparing this with the more extensive research that has often been carried out on other mammalian species strongly suggests extensive evolutionary conservation of many of the basic mechanisms operating within the social brain that regulate discrimination of individual identity, interpretation of emotion cues and even mate attraction.

The main aim of this theme issue has been to try to bring together the major advances made in recent years in diverse areas of research on both humans and other mammalian species investigating the neurobiology of social recognition, attraction and bonding. Numerous conferences and symposia have focused on specific features of social recognition, such as identifying individuals via odours or voices or faces, although research findings from the different senses are rarely presented together. Similarly, studies investigating the processes by which individuals recognize one another are often considered separately from those investigating communication and interpretation of emotional cues. Yet again, studies investigating these identity and emotion recognition cues often do not link into those investigating the specific cues that determine sexual or social attraction and can lead to the establishment of social bonds.

A number of the papers in this issue detail the present state of knowledge on the best understood area of social identity recognition in mammals, namely olfaction. The first provides a review of the nature of mammalian social chemo signals and the odorant receptors, neural pathways and neurochemical systems required for their detection by both the vomeronasal and main olfactory systems (Brennan & Kendrick 2006). The importance of genes in the major histocompatibility complex for determining chemosensory individuality is discussed in the context of recognition and mate choice in both mice and humans. The review also provides insights into the nature of learning-induced changes which occur within these systems in both rodent mate recognition and sheep models of offspring recognition. The second review focuses on a recent series of brain imaging studies on pair-bonding marmosets revealing that social odours which signal reproductive state influence not only sexual arousal and brain regions mediating the sexual response, but also those associated with memory and emotional decision making as well (Snowdon et al. 2006). This paper also discusses evidence for similar roles of social odours in the control of human reproduction, although it is clear that odour plays less of a role in humans than in many other species. A later review discusses the effects of neuropeptides that promote pair-bonding in voles on recognition and memory for social odours (Hammock & Young 2006). Evolutionary aspects of the shift away from more hard-wired utilization of olfactory signals to stimulate social and reproductive behaviours in a relatively inflexible manner, towards a more multi-sensory-based flexible system in primates, are discussed in Broad et al. (2006).

While vocal recognition may well be quite extensive among mammalian species, it remains the least investigated of the senses. However, exciting new brain imaging experiments have been carried out in humans and a single extensive review has detailed these together with a small number of behavioural and neurophysiological studies in monkeys (Belin 2006). This paper concludes that while voice identification in humans is less accurate than that for faces, the right brain hemisphere appears to be important for both, and particularly the superior temporal sulcus. Evidence is provided for the presence of specialized parts of this region for voice recognition. Interestingly, autistic humans do not seem to have these voice selective regions; their brains may process voice and non-voice sounds in the same way. This appears to contrast somewhat with the human face recognition system, where regions controlling the interpretation of face emotion rather than face identity recognition seem to be impaired in autistic individuals (Skuse 2006).

By contrast with the recognition of voice identity, there have been a large number of studies carried out on processing of face identity, face emotion and face attraction cues in humans, monkeys and sheep. A number of reviews in the current issue discuss these studies (Cornwell et al. 2006; Kanwisher & Yovel 2006; Skuse 2006; Tate et al. 2006). The first of these focuses on the considerable amount of behavioural,
Processing (Kanwisher & Yovel 2006). The authors argue strongly that there is a face-specific domain despite recent claims that this is just a region involved in expert recognition of any visual object. They also discuss a number of ways that this region may compute and represent faces. A further review considers brain imaging and neuropsychological experiments establishing the role of the amygdala and the different visual pathways projecting to it for processing face emotion in humans (Skuse 2006). It describes both a subcortical preconscious pathway activated by direct eye and a more cortical-based one for more detailed analysis of face emotion cues, as well as differential roles for the left and right brain hemispheres. Potential contributions of the serotonin transporter gene and X-linked genes in the integration of these two pathways and progress towards an understanding of genetic contributions to affective disorders are discussed.

Staying with the theme of human face perception, a further paper describes new experiments investigating developmental influences on male preferences for highly feminized female faces and female preferences for highly masculinized ones (Cornwell et al. 2006). The authors show that the degree of this dimorphic preference is correlated with the age of first sexual experience and they discuss possible hormonal and learning factors that might contribute to this phenomenon. Experiments also demonstrate that female attraction to specific male faces can occur independent of masculinity cues.

A final review on face recognition, attraction and emotion concentrates on behavioural and neurophysiological studies investigating these in non-human primates and sheep (Tate et al. 2006). This provides strong evidence for similar specialized encoding of face identity in these species and details electrophysiological experiments illustrating high-order view invariant coding by face sensitive cells both in the temporal and the frontal cortices and which may also be important for face imagery. The paper suggests that configurational aspects of encoding are perhaps primarily mediated by cells which respond to faces in a view-dependent manner. Research in sheep and monkeys is also discussed which shows evidence for the use of face emotion cues and encoding of these within the temporal cortex. The findings suggest that both identity and emotion cues are processed by parts of the temporal cortex, although emotion cues may be given priority compared with those for identity. The review also describes experiments using novel multiarray electrophysiological recording approaches, which suggest the presence of population encoding of faces by temporal cortex networks combined with high-order sparse encoding.

The remaining reviews in this issue deal mainly with the neurohumoral control of sociosexual behaviours, mate attraction, mate and parental bonding, and how sensory cues are used in this context. These start with a detailed consideration of how different aspects of the mammalian sexual response are controlled, focusing particularly on humans (Fisher et al. 2006). The authors propose that there are distinct, although integrated, systems in the mammalian brain for controlling the sex drive, individual mate attraction and bonding, and they provide a description of the key brain pathways that may be involved. They draw particularly on results from recent brain imaging studies and also rely on far more extensive studies carried out on other species (see Hammock & Young (2006) for bonds between mating partners). The brain imaging studies have also used faces of loved ones as a key stimulus and suggest a strong link with dopaminergic brain reward systems. Interestingly, this relationship has also been shown with female sheep viewing the faces of particularly attractive males, although in a strongly hormone-dependent fashion (Tate et al. 2006). Finally, the review provides new data showing that when a romantically rejected individual views a picture of the person who rejected them, this activates the same brain regions as in individuals performing tasks involving high risks. Indeed, one might argue that the quest for finding and reproducing with an appropriate mate represents the most high-risk social behaviour that any individual of any species engages in.

The next review continues with the theme of bonds between sexual partners by providing a detailed consideration of the roles of oxytocin and vasopressin systems in the brain of pair-bonding voles and their important links with dopaminergic reward systems and noradrenergic systems involved in olfactory recognition (Hammock & Young 2006). This animal model has often been considered somewhat esoteric but it has nevertheless produced some remarkable insights into what distinguishes social brains from asocial ones. Indeed, the authors discuss a possible association between polymorphisms in the vasopressin receptor gene for autism in humans and as a possible contributor to the wide degree of individual differences in sociosexual bonding.

Another paper reviews a field that has made considerable progress using animal models in recent years, namely the control of maternal offspring bonds in mammals, particularly sheep and monkeys. This again emphasizes the important role of brain oxytocin pathways as well as of the endogenous opioid peptides (Broad et al. 2006). The evolutionary approach adopted outlines a gradual shift away from a strongly hormone-dependent olfactory-based recognition system towards a more flexible multisensory-based one. The authors argue that this is what has allowed a huge increase in the importance and complexity of social learning, particularly in humans.

The next two contributions discuss relatively newer areas of research in terms of behavioural and genetic aspects of social and emotional behaviours. The first presents findings in a field of growing interest, ‘social buffering’ (Kikusui et al. 2006). It describes experiments in both rodents and monkeys showing the stress/anxiety relieving effects of the social presence of a calm but not a stressed familiar conspecific. The findings once again illustrate the power of emotional communication between animals in the control of behaviour. The review also discusses ‘social buffering’ in the context of human behaviour. The final review also discusses a relatively new field, namely the importance of imprinted genes for social behaviour (Isles et al. 2006). The authors summarize how
these monoallelically expressed genes may be used by the different sexes to promote various aspects of nurturing and social behaviours as well as growth in their offspring. This review also complements the earlier review in the issue that discussed the possible importance of X-linked genes for the control of interpretation of emotional cues (Skuse 2006). It seems likely that future research in this field of imprinted genes will reveal important new molecular candidates with key contributions to the control of the functioning of social and emotional brain, and perhaps also for the treatment of affective disorders in humans.

A final review by Jean-Pierre Changeux (Changeux 2006), and based on his Ferrier lecture, describes work investigating molecular contributions to the elementary building blocks of consciousness using genetically modified mice. This focuses particularly on the role of the nicotinic acetylcholine receptor in the brain and functions such as behavioural flexibility and exploration in both social and non-social contexts. Increasing dependence upon social behaviour and interactions is widely thought to have been an important driver for the evolution of higher levels of consciousness in animals.

Overall, there can be little doubt that we still have much to learn about how the brain controls different aspects of individual recognition, attraction, interpretation of emotional cues and the formation of social bonds. However, I hope that the excellent reviews in this issue will both promote debate and stimulate further research to address the significant gaps that still remain in our understanding.

Rewarding social interactions and relationships are of paramount importance for humans as well as for many other mammals, and yet we humans, in particular, seem highly prone to social and emotional dysfunctions. Indeed, in many cultures, this seems to be on the increase. Not only are there a wide range of psychiatric and developmental disorders associated with problems in social interactions and interpreting emotional cues, but also the changing face of many human cultures is progressively exposing problems with forming successful social relationships and bonds. Increasing numbers of individuals are leading single lives as both social and work pressures combine to make it difficult to find suitable partners. Along with this goes the rise in more asocial pursuits, such as playing computer and electronic games. In this respect, it is perhaps interesting to speculate what evolutionary selection pressures might occur in future human populations which could promote the development of a less social species. After all, it is a remarkable observation that a polymorphism in a single gene can lead to an asocial as opposed to a social species of vole (Hammock & Young 2006). So, perhaps a social bonding phenotype is not that stable an adaptation in humans either?

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REFERENCES


