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Intelligent perception

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Abstract

For an animal from any species to exhibit intelligent perception it must be capable of being consciously aware of what it perceives and capable of learning from this experience. Although many organisms, and for that matter machines, are capable of rapid adaptive learning in response to perception of environmental changes, such adaptations can occur without them being consciously aware either of external stimuli or their response to them. While behavioural and neurophysiological evidence suggests that, apart from ourselves, other higher primates must also be capable of such awareness, an important central question is whether such awareness is a characteristic of primate evolution or if it also occurs in sub-primate mammals as well. In this review I will examine our behavioural and neurophysiological evidence from visual and olfactory recognition studies in the sheep to support the argument that they are likely to be aware of and learn about both social and non-social objects and that they are therefore capable of intelligent perception. However, the impact of motivational changes on these perceptual processes suggests that they may be limited in terms of both prospection and retrospection and dealing with symbolic associations. © 1998 Elsevier Science B.V. All rights reserved.

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1. Introduction

For the purposes of this review I will define intelligent perception as the ability of an animal to exhibit adaptive learning responses to what it is consciously aware of in its environment or of itself. That is, intelligent perception is the ability to both be aware and to learn from it. The first major question to pose therefore when considering the possibility of intelligent perception in non-human animals relates to their capacity to be conscious of what they perceive. While the ability to detect, respond and even adapt to

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the presence of changing patterns of light, sound, smell, touch or temperature is an essential first step in conscious perception of the environment it is not sufficient evidence for its occurrence per se. This is because such abilities, even though they may be suggestive of thought processes, can often be readily displayed by simple micro-organisms and computer and robot sensors where conscious awareness clearly does not occur. While there is a remarkable resemblance in the gross structure and circuitry of the brains of advanced mammalian species to those of their human counterparts it is difficult to argue objectively that they must therefore experience the same degree of conscious awareness as ourselves. For example, a counter-argument that can be made is that just as there are enormous differences between the cognitive abilities of humans and other mammalian species then, despite even marked similarities in brain structure, the same level of disparity should be true for awareness. Nevertheless this latter argument does leave open the counter-proposal that if awareness has gradually evolved, as William James originally suggested (James, 1879), then many mammalian species must have the capacity to experience at least some even rudimentary form of awareness just as they also certainly have some rudimentary cognitive abilities.

To establish experimentally if any non-human species is capable of conscious awareness, and therefore intelligent perception, we need to first determine what particularly distinguishes conscious awareness from simple stimulus-response behaviour. A number of definitions of awareness have evolved mainly from the field of human psychology and normally involve its division into different hierarchical levels with increasing degrees of complexity (Young, 1994). However, at this stage in dealing with non-primate mammals we are more concerned with the critical problem of determining experimentally whether they are capable of conscious awareness, and therefore intelligent perception, at all. To achieve this important first step we have first to find what particularly distinguishes conscious awareness from straightforward stimulus-response behaviours. It could be argued that one of the major factors that distinguishes conscious from unconscious perception is the ability of an organism to simultaneously perceive and experience external or internal stimuli. That is, in simplest terms, conscious in contrast to unconscious awareness implies the ability to feel some form of emotional response to what is perceived. In humans we know from our own experience that conscious awareness can occur in the absence of an overt emotional response but in other animals this possibility would be difficult to distinguish empirically from simple unconscious stimulus response behaviour. Indeed, I will argue later that it may be this ability of humans to be aware of objects without necessarily experiencing an emotional reaction that is the key to our ability to exhibit such sophisticated skills in intelligent perception.

A number of complex behaviours are highly suggestive of conscious perception in mammals, such as self-recognition in mirrors, social communication, individual recognition of conspecifics, deceit and empathy, emotional expression and complex learning (particularly rule-following). However, reasonable evidence for many of these behaviours has only been provided in higher primates and even in these cases experiments are often open to re-interpretation due to limitations in the experimental paradigms used (Heyes, 1994; Kendrick, 1997). One way forward in trying to establish intelligent perception in non-human mammals is to combine such behavioural assessments with a consideration of how an animal's brain is organised to process sensory information from the environment. Where possible this can then be contrasted with what is known about how the human brain functions under similar circumstances. Such a neurobiological approach to understanding consciousness has also been put forward by others (Crick and Koch, 1990). Recent advances with functional brain imaging techniques using magnetic resonance imaging (MRI) and positron emission tomography (PET) have allowed studies to be conducted in humans aimed at understanding which brain regions are functionally active during actual perception of objects and whether these are the same or different from those which are active when an individual forms a mental image of them. Results from these studies together with those from the neuropsychological literature derived from brain damaged patients have repeatedly shown that there is considerable overlap between brain regions which are activated during direct perception of objects and when mental images are formed of them (Farah, 1995; Kanwisher et al., 1996; Koch and Braun, 1996). There is not, of course, complete overlap as illustrated by the phenomenon of 'blindsight' in humans where brain damaged patients can still be respond appropriately to objects without actually being aware of them (Milner and Goodale, 1995). In some cases it has even been claimed that visual imagery even involves the primary visual cortex (Le Bihan et al., 1993; Kosslyn et al., 1995) although others have disputed this (Crick and Koch, 1995). In general, imaging studies in humans and supportive electrophysiological experiments in monkeys have suggested that visual awareness is mediated primarily via the so called 'what' pathways in the brain as opposed to the 'where' pathways which are less associated with such awareness. These pathways respectively underlie object identification and the determination of spatial location (Ungerleider and Haxby, 1994; Milner and Goodale, 1995; Koch and Braun, 1996). They are also relatively anatomically distinct after the primary visual cortex, the 'where' pathway occupying a dorsal course involving the posterior parietal cortex and the 'what' pathway occupying a more ventral course involving the inferotemporal cortex. The implications of this research are therefore that if we can show that the brain of a non-human animal species processes complex sensory information from objects in the same way that the human brain does then that animal species should have at least some capacity to form mental images of them in their absence and hence be consciously aware.

Another way in which a detailed study of how an animal's brain is organised may allow us to imply that it is consciously aware is to establish how sensory analyses of objects are influenced by their potential emotional significance. That is, if we can either show that an animal is likely to simultaneously experience pleasure or distress when it perceives an object and/or if the way sensory information is encoded by the brain suggests a strong organisational influence of the emotional significance of objects this would also imply that the animal is consciously aware of them.

We have used such a combination of behavioural and neurobiological approaches to investigate the extent to which conscious awareness, and hence intelligent perception, can be displayed by an advanced non-primate mammal, the sheep. We have concentrated both on the ability of these animals to perceive highly salient non-social objects such as food and also on aspects of their social cognition pertaining to their ability to recognise the sight or odours of specific individuals.

2. Visual recognition and learning

Although with their laterally placed eyes sheep have almost all round vision they only have good visual acuity in their binocular eye-field (40–60°). This visual acuity has been estimated to be in the region of 3–4′ (see Piggins, 1992) which places it between that of a cat and a monkey, although it is possible that it may be better for moving rather than static objects (Backhaus, 1959; Clarke and Whitteridge, 1976). Sheep may even have colour vision (Alexander and Shillito Walser, 1978b; Alexander and Stevens, 1979). It should therefore be possible for sheep to learn to recognise many salient objects in their environment using visual cues. The main question in terms of intelligent perception is whether they are actually consciously aware of these objects.

2.1. Behavioural studies on perception of objects

In operant experiments it has been shown that sheep, along with goats and cattle, can learn to visually discriminate between geometric shapes that either differ in their appearance or orientation in order to gain a food reward (Baldwin, 1981). We have also shown that they can learn to discriminate between geometric shapes in a Y-maze (Kendrick et al., 1996). Relatively little research has specifically addressed the ability of sheep to visually discriminate non-social objects in their environment. However, they do use visual cues for recognising food and do not have any problems in discriminating between foods if they are anosmic (Baldwin et al., 1977; Milne et al., 1982). Indeed, behavioural studies have shown that selective and preferential grazing of clovers and different types of grass, as well as choices between hay and concentrates can be made using visual cues (Kendrick and Baldwin, 1986; Bazely, 1988). Interestingly, the speed and duration of learning for natural objects like food (and also faces which will be discussed later) is much better than for geometrical symbols or meaningless objects like coloured bottles. Thus a sheep will learn to visually recognise a new palatable food in one or two trials and will retain this information for 3 months or more. Lambs have been shown to retain learned information about unpalatable foods for over 3 yr (Green et al., 1984). On the other hand similar learning to associate geometric symbols or novel objects with food can take anything from 10–40 trials and learning is often only retained for a few days or even a few hours in some circumstances (Kendrick, 1992; Kendrick et al., 1996).

2.2. Neural control of object recognition

Our neurobiological experiments have established that sheep (Kendrick and Baldwin, 1986), like primates (Burton et al., 1976; Mora et al., 1976; Rolls et al., 1976), have specialised neural circuits in the zona incerta and lateral hypothalamus of the brain which respond to the sight of foods and whose activity reliably reflects individual behavioural preferences for specific foods. Indeed, the activity of these cells in response to the sight of different food objects almost perfectly predicts whether an animal will actually eat a particular food. In support of our behavioural observations we have shown that these neural circuits rapidly adapt to respond to the sight of novel foods (within 1–2 trials) and this responsivity is maintained for several months or more even though the animals have not seen or eaten the food again (Kendrick, 1992). However, while the cells will also adapt to respond to the sight of unfamiliar objects (coloured bottles) associated with a food reward this takes many more trials (usually >10) and the responsivity is only maintained for a few hours or so. This clearly illustrates how this animal's brain is adapted to efficiently learn associations between natural objects and reward but not novel associations between artificial objects and reward.

It seems probable that the activity of neural circuits that respond to the sight of food is associated with the animal being aware of the food. The main reason for this is the fact that the regions where these cells are found are within the so called 'reward' centres in the brain. That is, animals will voluntarily self-stimulate themselves through electrodes implanted in them and in rhesus monkeys it has even been shown that individuals will stimulate themselves through microelectrodes that are recording from these cells which respond to the sight of food (Rolls et al., 1980). Sheep have also been shown to self-stimulate through electrodes placed in these same regions (Baldwin and Parrott, 1982). Thus it seems likely that when these cells are activated in response to the sight of a palatable food the animals simultaneously experience a pleasant feeling.

These cells that respond to the sight of food in the lateral hypothalamus and zona incerta of both sheep and monkeys rarely respond to its ingestion. Thus it seems possible that when the animals see a palatable food they are simultaneously aware of an associated pleasurable response to it which is distinct (neurally) from any pleasurable response associated with its actual ingestion. That is, visual and taste awareness are separable, as would be predicted if the animals, like us, are capable of independent awareness of different sensory modalities.

One of the implications of these neurobiological investigations of neural circuits involved in food recognition is that since they fail to respond to unpalatable foods or to palatable foods to which the animal is satiated then such stimuli might fail to have any impact in terms of awareness. While it is possible to argue that different neural circuits deal with awareness of stimuli that the animals are not currently attracted to, it may be that in sheep conscious awareness is mainly limited to objects that are desired at any point in time and that other objects are simply ignored by a form of highly focused selective attention. In this respect it is interesting to note that in sheep many cells in the zona incerta which normally respond selectively to food objects when the animal is hungry will switch to responding to the sight of salt or salt solutions when its primary motivation is to ingest sodium (Kendrick and Baldwin, 1989b). I will return to this point later in experiments we have carried out on the effects of motivational changes on the neural control of social recognition.

2.3. Behavioural studies on recognition of faces and body shapes

The first experimental evidence that visual cues from the head region might be important for individual recognition in sheep was the demonstration that maternal ewes found difficulty in recognising their lambs at a distance when the appearance of the whole body or the head region alone was altered (Alexander and Shillito Walser, 1977). Other evidence for face and/or body shape recognition comes from studies indicating that sheep even respond to the sight of their image in a mirror. Under these circumstances they react as if they are encountering another unfamiliar sheep (i.e., they do not show evidence of self-recognition) and this influences their behaviour in raceways (Franklin and Hutson, 1982) and reduces their endocrine and behavioural responses to isolation (Parrott et al., 1988).

More recently, with the use of a two-choice Y-maze, we have shown that sheep can discriminate between the projected images of faces of different sheep and humans (Kendrick et al., 1995). However, discriminatory performance declines considerably if the faces are presented inverted and to a lesser extent if the eyes are obscured or the face presented in profile. Monkeys on the other hand seem to be rather better at discriminating inverted faces which may reflect their arboreal habitat where individuals are often viewed upside down (Rosenfeld and Van Hoesen, 1979). However even monkeys take longer to discriminate inverted than normally oriented faces (Perrett et al., 1988). The internal organisation of facial features does not appear to play a major role in visual discrimination between sheep and human faces although the speed of the choice of the sheep face is significantly retarded under these circumstances.

In order to establish whether sheep can actually recognise individual conspecifics from their faces we have also carried out a number of other experiments using a Y-maze. In the first instance we have shown that ewes can distinguish between the faces of familiar male and female sheep by observing that they will chose to selectively approach a male face when they are in oestrus, whereas they will approach a female face when they are in anoestrus. Similarly we have shown that they will approach a face of an unfamiliar female of their own breed in preference to one of another unfamiliar breed (Kendrick et al., 1995, 1996). Another group has also shown that images of familiar conspecifics alleviate fear responses more effectively than images of individuals from a different breed (Bouissou et al., 1996). Interestingly, we have found that inverting faces impairs discrimination learning performance only if faces of a familiar breed are used and not if those of an unfamiliar breed. There is also no discrimination learning deficit shown with inverted images of highly familiar non-social objects. This mirrors the facial inversion effect that has been extensively described in humans and which has often been used as evidence that the brain is specially organised to discriminate familiar types of faces compared with other types of objects (see Kendrick et al., 1996).

Maternal ewes can distinguish images of their lambs faces from those of strange ones in a Y-maze although it generally takes a long time for them to learn to do this (2–4 weeks). This may be due to the small size of the lambs face and relative homogeneity of their facial features compared to those of adults (Kendrick et al., 1996). When ewes are trained to distinguish between two adult ewe faces in order to receive a food reward they can usually do so with remarkable speed (< 20 trials) given the complexity of the task. As in the case of familiar non-social objects, like food, they are also better at learning to discriminate between unfamiliar faces than they are between unfamiliar objects such as geometrical symbols. The speed of discrimination learning is also much faster between the faces of socially familiar animals than for unfamiliar ones of the same breed (Kendrick et al., 1996). This suggests that the brain is organised in such a way that it is easier to learn new rewarding associations with familiar faces than unfamiliar ones, presumably because the familiar faces are already optimally encoded by the brain.

Finally, we have obtained evidence that sheep appear to be able to form a ‘mental representation’ of other individuals. Thus if they are trained to associate a frontal view of a familiar individual with a food reward they will also associate a profile view of that same individual with the reward without receiving any further training (i.e., they would appear to know that the profile view is of the same individual whose frontal view they had been trained with—Kendrick, Leigh, Hinton, Peirce and da Costa, unpublished observations). The ability to form such mental representations of individuals strongly suggests that the animals are capable of being aware of them.

While sheep are born with a fully mature and functional visual system they do not appear to be able to use it to identify important individuals, like their mother, from their faces for a month or more. Thus although within the first 24 h after birth they will show a preference for properly configured faces, like human infants, it would appear that there must be experience dependent changes occurring within neural pathways involved in the identification of specific faces that take a month or more to become fully functional.

Sheep obviously cannot rely on facial discrimination entirely to visually distinguish different individuals in their environment, especially at a distance. Cues from body shape, posture, appearance and movement probably also play an important role in this context although few investigations have been made to prove this experimentally. Lambs, for example, find it difficult initially to recognise their mothers when the latter are shorn (Alexander and Shillito Walser, 1978a). Sheep in raceways in stock yards have also been shown to respond differently to projected images of front, side and head on views of other sheep (Franklin and Hutson, 1982), suggesting that visual cues from the body are important both for recognising other sheep and deciding whether to follow or avoid them. We have recently found that humans can approach much closer to flocks of Dalesbred sheep if they adopt a quadrupedal as opposed to a bipedal posture although, at close range, eye-gaze is also important and humans can approach closest if eye contact is avoided (Kendrick, 1994)

2.4. Neural control of face recognition

In humans the neural substrates involved in processing identity of individuals from their faces strongly involve the ventral ‘what’ processing pathways, particularly the inferotemporal cortex, which are associated with visual awareness (Sergent and Signoret, 1992; Ungerleider and Haxby, 1994; Kanwisher et al., 1996). Indeed, a recent functional MRI study has confirmed that the same region of the right anterior inferotemporal cortex is activated during both direct perception of and mental images of faces (Kanwisher et al., 1996). We have now established that there is a similar pattern of activation involving these ventral pathways during face-recognition in the sheep. While we cannot use functional imaging techniques such as PET and MRI we can use even more sensitive techniques which involve quantifying changes in the cellular expression of genes, such as c-*fos*, which are rapidly and strongly activated in the brain during synaptically-induced increases in electrical activity. Using this approach we have exposed sheep to a visual discrimination between human and sheep faces in a Y-maze under conditions where they could or could not perform the task. Our results have shown that when animals successfully performed the task and chose the sheep face this was associated with extensive increases in c-*fos* mRNA in primary visual processing regions such as the lateral geniculate nucleus, areas VI and V2 of the visual cortex as well as in secondary association regions such as the orbitofrontal, parietal and cingulate cortices (Fig. 1). There was also extensive activation in limbic regions associated with emotional responses (medial and lateral amygdala, entorhinal cortex, septum, diagonal

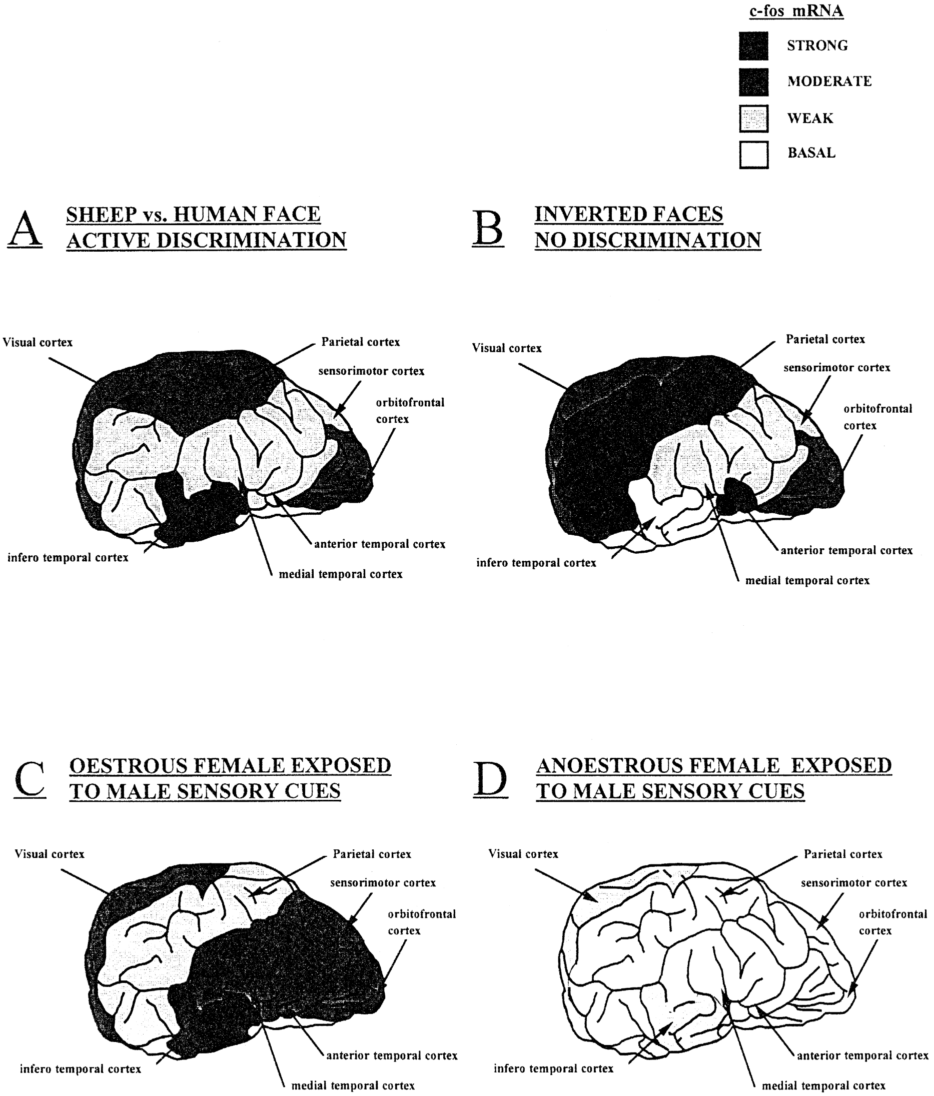

Fig. 1. Schematic diagrams of the sheep brain showing cortical areas that are activated (as evidenced by quantifying increased expression of c-*fos* mRNA) during a successful visual discrimination between a sheep and a human face (A) and when discrimination was prevented by inverting the face images (B). (C) shows the pattern of activation when a female is exposed to the sight of a male when she is in oestrus and (D) when she is in anoestrus.

band of broca, hippocampus and dentate gyrus). This activation pattern therefore strongly suggests that the animals were both perceptually aware of the faces and their emotional significance. On the other hand if the faces were presented inverted (which the sheep failed to discriminate between) the pattern of activation in the association cortex and limbic system was very different (Fig. 1). The parts of the temporal cortex normally particularly associated with face recognition were not activated and instead there was a stronger activation in more dorsally located regions in the parietal cortex. There was also little evidence for activation in limbic regions (Broad and Kendrick, unpublished observations). Thus it would appear that inverted faces were being processed by the brain as if they were unfamiliar non-face objects with no immediate emotional consequence.

The attractiveness of different individuals can of course vary quite considerably and therefore we have examined what impact changes in motivational state can have on the way the brain responds to visual cues from the same individual when it is attractive as opposed to when it is not. To do this we have contrasted the patterns of c-*fos* expression in the brain of a female sheep exposed to visual cues from a male when she is sexually attracted to him (behavioural oestrus) as opposed to when she is not (anoestrus) (Ohkura et al., 1997). In this case while visual cues from the male increase c-*fos* expression in the same regions as during the facial discrimination task described above and additionally in areas of the hypothalamus known to be important for mediating receptive, proceptive and endocrine responses towards the male (mediobasal hypothalamus, medial preoptic area, paraventricular nucleus). When the female is exposed to a male but is not in behavioural oestrus, c-*fos* expression is unaltered not only in the hypothalamic and limbic regions which contain sex steroid hormone receptors and which mediate sexual behaviour responses, but also in areas of primary and association cortex visual processing regions (i.e., visual cortex, temporal cortex and orbitofrontal cortex) which do not (Fig. 1). Presumably, the pathways which feedback to these sensory processing regions from those mediating behavioural responses, alter their sensitivity to visual cues from the male. The failure of male visual cues to activate the parts of the ventral processing stream that normally respond to faces, and which are associated with awareness, suggests that the females may not even be consciously aware of the male at this time. Thus, this is further striking evidence that motivational changes in the sheep may dramatically alter even its awareness of external stimuli.

Electrophysiological studies have also given us important insights into how the sheep brain processes visual information relevant to individual recognition. This approach has established that the sheep primary visual cortex (V1 and V2) has the same cell types, including binocularly driven cells, as have been described in the monkey (Clarke and Whitteridge, 1976; Clarke et al., 1976). Unlike the monkey however, the primary visual cortex of the sheep is fully developed and functional at birth (Ramachandran et al., 1977), which is in keeping with the fact that, as a precocial mammal, it has to be able to use its visual sense to learn about and recognise important aspects of its environment right from the beginning of its post-natal life. Our own electrophysiological experiments have concentrated on whether the temporal cortex of the sheep, like that of the monkey (Gross et al., 1972; Bruce et al., 1981; Perrett et al., 1982, 1984, 1988, 1992, 1987), is part of a neural system which is involved in visual recognition of complex images such as faces and body shape. These electrophysiological experiments have confirmed that there is indeed a small population of cells in the temporal cortex of the sheep which respond preferentially to projected images of faces and that different sub-populations of cells code for faces with a common social significance (Kendrick and Baldwin, 1987; Kendrick, 1990a,b, 1991, 1992). Thus one group of cells responds to faces of sheep, or of other animals, with horns, and their activity is influenced by the size of the horns. In sheep, and other horned ungulates, the presence and size of horns provides important information concerning dominance and gender (Collias, 1956; Geist, 1968; Lincoln, 1972). Another group of cells responds preferentially to faces of sheep of the same breed, and particularly socially familiar animals. Sheep form consortships with specific individuals and prefer to stay with members of their own breed (Winfield and Mullaney, 1973; Shillito-Walser et al., 1981; Arnold, 1985) and our own behavioural studies have shown that they prefer to approach facial images of members of their own as opposed to another breed (Kendrick et al., 1995). Lastly, another group of cells responds equivalently to human and dog faces, the two species which represent the greatest potential threat to sheep and which they will generally avoid. The fact that these temporal cortex cells code for faces of different social significance suggests that their responses have been modified by experience. Finally, in confirmation of our behavioural and neuroanatomical experiments we have found that these facial responsive cells do not respond well to faces presented inverted or in profile (Kendrick and Baldwin, 1987; Kendrick, 1991, 1992).

The cues that are being used to distinguish between different faces are still the subject of investigation, although we have managed to establish a few important principles. It is clear that these temporal cortex cells are mainly coding for specific categories of individuals, rather than different individuals per se. There is so far, for example, no evidence of differential responses to faces of specific individual humans or sheep even though we have behavioural evidence that they are capable of recognising at least 10 or more individual sheep (Kendrick et al., 1996). The different categories of individual that are being responded to by separate populations of cells are probably encoded on the basis of a number of particular facial features and conformations. We have found, for example, that the cells responding to faces with horns are profoundly influenced by the presence of eyes but not the species of the face (Kendrick, 1994). Thus, horned animals viewed from the back, or from the front but with their eyes obscured, are not very effective stimuli, although a frontal view of a goat or a human face with horns is. Specific features are also important for cells encoding the sight of a human or dog face. In this case the important features seem to be a correctly orientated profile and the presence of the eyes (Kendrick, 1991). Interestingly, however, the activity of cells responding to human faces is not altered by adding horns to the image of the face. It would therefore appear that the coding strategy of these latter cells is more sensitive to the specific species identity of faces and therefore not influenced by simply incorporating some sheep-like features in the facial image.

There may be some aspect of sequential or hierarchical processing of different features in facial images by these temporal cortex circuits (Kendrick, 1994). At the earliest level of processing face-like images would be distinguished, based on simple general features such as face outline, eyes and orientation. At the next level of processing, cells would encode for facial images possessing simple secondary features, such as horns. Finally, cells representing the most complex level of processing would encode a number of specific tertiary features that distinguish particular classes of individuals and possibly even specific individuals. Plastic changes associated with altered social recognition priorities should primarily occur at this most complex processing level, although this has yet to be shown.

In sheep there is clearly an overriding influence of social and emotional significance on the coding strategies employed by cells responding to faces, and they appear to be tuned to respond to only limited views of the face. In monkeys, while there is similar evidence of the influence of social and emotional significance on the responses of cells in the temporal cortex, this does not appear to be as extensive as in sheep and many different types of cells can be found with responses to a variety of different views and orientations of faces and which can code differentially for a variety of familiar and unfamiliar individuals (Perrett et al., 1984, 1992). Behavioural evidence also suggests that monkeys may be better at discriminating between faces under more diverse viewing conditions and orientations (Rosenfeld and Van Hoesen, 1979). A number of face-responsive cells in the temporal cortex are also sensitive to facial expressions (Haselmo et al., 1986, 1989; Perrett et al., 1984, 1992) and primates, unlike sheep, obviously make wide use of facial expressions for social communication.

Overall, these findings suggest that, in primates, the function of the temporal cortex is mainly to process sensory information relating to recognition of a large number of individuals and the social signals they display. In contrast, the main function of this brain region in the sheep may be to identify primarily categories of individuals that have similar social or emotional significance, and only to identify a small number of specific individuals. The overall changes in the size and topography of the temporal lobe in primate evolution may be a reflection of a social requirement for this more complex requirement of individual visual recognition of many different individuals and their expressions.

This increased requirement for visual recognition of individuals might have only been possible at the expense of partially sacrificing a limited coding strategy of hard-wiring individual recognition with emotional responses. For the animal species that have adopted a strategy of organising perceptual categories primarily on the basis of their unique emotional or behavioural significance they would have a limited capacity to recognise large numbers of specific individuals although they would have a very efficient system for ensuring appropriate responses to a limited number of important things in their environment. For animal species that have adopted a more complex feature detection strategy, which is not hampered by restrictive organisational influences of emotional significance, a major consequence would be that many different individuals could be discriminated between and viewed, or thought about, without necessarily evoking a behavioural or emotional response to them. One potential adverse result of abandoning, or reducing, a close-link between recognition and emotional responses would be that the ability to show suitable emotional responses to different individuals, and their expressions, might be compromised. This is obviously one of the major characteristics of autism and schizophrenia in humans for example. On the other hand the obvious advantage in disassociating percept from affect is to allow the development of high order cognitive skills using abstract concepts and rules which is a major feature of primate evolution. Indeed, a feature of the many different definitions of human cognition has been the absence of any mention of affect.

One result of directly interlinking the neural organisation of sensory recognition and affect might be that early formative emotional experiences and attachments could have major consequences for social and sexual preferences throughout an animal's life by producing an irreversible bias in an animals' recognition priorities which would preclude any possibility of developing alternative priorities in the light of later experience. Certainly, cross-fostering experiments in sheep and goats (Kendrick, Houpt, Hinton and Skinner, unpublished observations) have demonstrated profound, irreversible, alterations in social and sexual preferences towards the maternal as opposed to genetic species as a result of being raised by a different species. Indeed the overall result of having a recognition system organised on the basis of emotional salience would be to reduce the potential for plasticity in the system. One way around this is to let humoral events dictate rapid alterations in response priorities by simply switching between them. We have shown, for example, that such reversals in recognition priorities do occur in the context of oestrus (in terms of interest in male sensory cues) and in appetite where the same cells in the zona incerta can rapidly change their responsiveness to the sight of food and salt depending upon the animal's motivational priorities (Kendrick and Baldwin, 1989b). We also have similar evidence from the olfactory system in the context of post-partum lamb recognition which will be discussed later (Kendrick et al., 1992a,b).

Unfortunately no studies either in monkeys or sheep have attempted to identify whether cells in the inferotemporal cortex that respond preferentially when animals view faces might also be active when mental images are formed of them. Functional MRI studies in humans strongly suggest that this would be the case for cells in this corresponding region of the human brain (Kanwisher et al., 1996). In general, face-responsive cells in these both monkeys and sheep only show increased activity during the actual presentation of faces. There is not, for example, strong evidence that they continue to show increased activity even for short periods after the face images disappear. It will obviously be interesting to investigate whether increased activity in such cells can occur in response to either visual or non visual cues that predict the appearance of faces. If this were to be the case then it would potentially provide further neurophysiological support for the hypothesis that both monkeys and sheep are, like ourselves, consciously aware of the individuals they perceive.

2.5. Neural control of recognition of body shape and attributes

In line with our behavioural experiments suggesting that sheep may recognise humans using cues from body shape and posture we have found a population of cells in the temporal cortex which responds preferentially to the sight of a human body shape (Kendrick and Baldwin, 1989a). Similar cells have also been reported in the monkey temporal cortex (Perrett et al., 1985). The majority of these cells only respond when the human shape is moving towards the animal although a small number respond to either retreating or stationary figures. Some cells even respond differentially to both approaching and withdrawing human shapes (i.e., excited by approaching figures and inhibited by withdrawing ones, or vice versa). Obviously an approaching human represents the most important stimulus for a sheep to attend to and it is not surprising that the majority of cells code for this. In agreement with our behavioural studies we have found that the responses of all these different cell types are both posture and view dependent with views of humans from the side, or crawling being relatively ineffective stimuli. Thus, it would appear that these cells responding to the sight of a human body shape, like those responding to faces, must be influenced by learning. Similarly, since they are also present in the same part of the temporal lobe as those responding to faces it seems likely that the animals are also potentially consciously aware of body images.

While the cells in the temporal cortex responding to human shapes are clearly broadly tuned to allow them to code for the various shapes, sizes and clothing that humans can appear in, we have also found a small number of cells that are strongly influenced by what humans are wearing (Kendrick, 1994). Thus, as with the cells responding to faces, only a very small sub-population of cells responding to the human body shape appears to be more finely tuned to perform a more complex visual discrimination. It seems probable that there are populations of cells in the temporal cortex which also code for different aspects of sheep body shapes and postures, since behavioural experiments have shown that visual cues from the body are important for these animals (Franklin and Hutson, 1982).

3. Olfactory perception

Olfaction is a much more primitive sense than vision and this is reflected by the fact that the brain is organised such that smell information reaches areas of the limbic system and hypothalamus governing motivational behaviours and endocrine responses with the minimum amount of processing. As such it may well be that although this sense is extensively used for identification of important social and non-social objects by non-primate mammals, in particular, it may not evoke high levels of conscious awareness and only fixed behaviour patterns. This must certainly be true of the accessory olfactory system which processes pheromones via the receptors in the vomeronasal organ and does not involve areas of association cortex involved in conscious awareness. It may not however be so true for the main olfactory system that processes air-born odours and which does access such regions, particularly the frontal cortex. The fact that it is difficult for us to perceive odours without experiencing a corresponding emotional reaction to them is also suggestive that other animal species should be aware of many of the smells they perceive. Indeed, as Kipling wrote—‘‘Smells are surer than sounds or sights to make your heartstrings crack’’ (from his poem Lichtenberg published in The Five Nations Collection, Methuen, London, 1903).

3.1. Behavioural studies

It has been claimed that rodents can demonstrate learning abilities using olfactory cues as complex as those of primates in recognising objects using visual cues. Certainly learning is extremely fast, although claims that this is due to the acquisition of the type of learning set (Slotnick and Katz, 1974) that is shown by primates with visual discrimination problems have been disputed (Reid and Morris, 1992). In sheep, there much data concerning olfactory recognition of individuals. They can, for example, during operant tasks, readily distinguish between odours from samples of wool, faeces, saliva and secretions from the interdigital pouch, the inguinal pouch and the infra orbital pouch collected from different individuals (Baldwin and Meese, 1977). Rams are able to distinguish between oestrous and anoestrous ewes using olfaction (Blissett et al., 1990) and the smell of rams or their wool can induce oestrous in ewes (Knight, 1983). The areas we have mainly been working on concern olfactory recognition of lambs by maternal ewes and olfactory responses to males by females.

Post-parturient multiparous ewes form a selective bond with their lambs usually within 2 h of having given birth to them and it is known that this selective bond is initially entirely based on the sense of smell (Poindron and Lévy, 1990). We have shown that the formation of the bond, like that of the actual induction of maternal behaviour itself, is triggered by feedback from the vagina and cervix reaching the brain. Thus, a post-partum ewe that has selectively bonded with her lambs can be induced to accept and rear an alien lamb by manual stimulation of the vagina and cervix for a few minutes (Kendrick et al., 1991). Also, both maternal behaviour and bonding are stimulated by manual stimulation of the vagina and cervix given to anoestrus ewes induced to lactate using hormone-containing vaginal sponges (Kendrick et al., 1992a,b). The source of the lamb's odour signature by which the ewe learns to recognise it, is now thought to be its wool and skin rather than the amniotic fluid (Alexander and Stevens, 1981; Poindron and Lévy, 1990). The odour signature must be highly individual since there is evidence that even the odour signatures of twin lambs are recognised differentially (Porter et al., 1991). While the ewe does eventually develop the ability to recognise her lambs visually (as already discussed) and vocally it appears that only mismatches in odour cues rather than visual or vocal ones will elicit an aggressive reaction by her towards strange lambs. Thus anosmic ewes will accept suckling attempts from any lambs (Baldwin and Shillito, 1974). This emphasises the close link between the olfactory system and the evocation of emotional behaviour responses.

3.2. Neural control of odour recognition

Neuroanatomical studies have shown that immediately after birth when the olfactory memory associated with lamb recognition is forming there is increased c-*fos* mRNA in the olfactory bulb (OB) as well as in secondary and tertiary olfactory processing structures such as the pyriform cortex, the orbitofrontal cortex, amygdala, septum and hippocampus (Da Costa et al., 1997). Once again similar patterns of activation have been reported in MRI studies in humans during conscious perception of odours (Koizuka et al., 1994). Our electrophysiological experiments on ewes during pregnancy and post-partum have shown remarkable changes in the responses of the mitral cells of the olfactory bulb (the cells which output olfactory information to the rest of the brain) as a result of giving birth to and bonding with a lamb (Kendrick et al., 1992a,b). None of these cells respond preferentially to lamb odours during late pregnancy, whereas 60% of them do so after the sheep have given birth and bonded with their lambs and this is associated with increased release of glutamate and GABA. Of these cells most respond equivalently to odours from either the ewe's own lambs, or from strange lambs, although a few show significantly greater responses to odours from own lambs. Thus, there has been a dramatic alteration in the coding priorities exhibited by the mitral cells as a result of a ewe giving birth and forming an olfactory memory of her lambs' odour signatures. This again suggests that the ewe perhaps only becomes aware of the smell of lambs when she has a motivational requirement to do so. Indeed, the same is true of female perceptions of male odour cues since, like the visual system processing of male visual cues, male odours also fail to have any impact on regions of the brain which respond to his odours when the female is attracted to him (Ohkura et al., 1997). Thus evidence from both the visual and olfactory system in the sheep suggests that motivational changes profoundly alter perceptual awareness.

Different odours are thought to be coded within the olfactory bulb through different patterns of activation (see review by Keverne, 1982) however, as with the visual recognition system that I have discussed above, there once again seems to be support for a hierarchical coding strategy, with a relatively small proportion of cells finely tuned to discriminate between the odour signatures of different lambs in contrast to a much larger population of cells that is broadly tuned to respond to lamb odours per se.

There also seems to be an important role of maternal experience in modifying the organisation of the olfactory bulb both in terms of its ability to respond to physiological inputs (vaginocervical stimulation) and pharmacological challenges (Keverne et al., 1993; Lévy et al., 1993, 1995). Thus, in primiparous ewes, vaginocervical stimulation fails to evoke the normal pattern of neurotransmitter changes seen in the olfactory bulb of maternally experienced ewes, but does so within 6 h of their giving birth to and bonding with their first lambs (Keverne et al., 1993; Lévy et al., 1993). These changes in the organisation and excitability of the olfactory bulb which result from a ewe's first maternal experience last for life, and may explain both why there are higher incidences of lamb rejection and slower selective bonding latencies shown by primiparous compared to multiparous ewes (Kendrick, 1994). Whether they also represent a heightened initial perceptual awareness of their lambs is an open question however.

4. Conclusions

While there are a number of important gaps in our understanding of whether or how different animal species perceive and are aware of objects and individuals in their environment we are nevertheless making progress. The complexity of social and object recognition skills exhibited by even non-primate mammals such as sheep combined with the evidence that their brains can process sensory information from such objects in a similar manner to our own is evidence in itself that they should be capable of being aware of them. The fact that brain regions involved in perception of these objects are strongly organised by or associated with emotional and motivational salience is further compelling evidence that the animals must simultaneously experience some form of emotive response to what is perceived. The precise degree of awareness that these animals are capable of is more difficult to assess although the strong influence that motivational relevance has on the animal's behavioural and neural response to specific social and non-social objects does suggest that their awareness is strongly governed by current priorities. As such, reflection on past events and prospective planning abilities may be somewhat limited and this of course would restrict the development of complex cognitive skills, such as those requiring analysis of a number of different past experiences in order to plan a novel future course of action. Similarly awareness of the use of abstract symbols or rules would be minimal since they would have no inherent motivational relevance. This does suggest that it cannot simply be the relative increase in human brain size during the course of social evolution that has led to our development of increased cognitive skills and awareness. Rather one might hypothesise that the increased requirement for specific recognition of both more social and non-social objects during primate evolution could only be achieved by weakening the organisational influence of motivation and emotion on perceptual processes. Once this weakening had occurred the primate brain would have rapidly become capable of developing cognitive skills requiring simultaneous awareness and manipulation of past experience in order to generate plans for future action. The use of abstract symbols and concepts, including language, would also have become a possibility.

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