

# BEHAVIOURAL AND NEURAL CORRELATES OF MENTAL IMAGERY IN SHEEP USING FACE RECOGNITION PARADIGMS

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**Abstract**

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*Determining objective measures for proof of consciousness in non-human animals has been helped by improved understanding of neural correlates of human consciousness. Functional imaging and neuropsychological studies have shown remarkable overlap between structures involved in actual perception of social and non-social objects and those involved in forming mental images of them. One area of particular interest is individual face recognition. This involves regions of the temporal lobe that are mainly only activated by actual perception or mental imagery of faces. Using behavioural, neuroanatomical and neurophysiological approaches in sheep, we have found that they have similar specialized abilities for recognizing many individuals from their faces. They have developed the same specialized neural processing regions in the temporal lobe for aiding such recognition. Furthermore, parallel activation of other brain regions controlling behavioural and emotional responses only occurs when they are overtly interested in the individuals whose faces they perceive. Such interest might therefore equate to their becoming consciously aware of them. Preliminary experiments have indicated that sheep may form and use mental images and that the regions of the temporal lobe that respond to faces can also do so under conditions where faces are suggested but do not actually appear. Such similarities between humans and sheep in this form of social recognition make it difficult to claim that humans can form mental images of faces whereas sheep cannot. While the ability to form and use mental imagery is not in itself definitive proof of consciousness, it is an important component part.*

**Keywords:** *animal welfare, brain, consciousness, face recognition, mental imagery, sheep*

## How can we approach the question of proof of consciousness in animals?

Are non-human animals capable of conscious perception? This has been a central question both for animal welfare and for neuroscientists using animals as models for understanding human brain function. While the ability to detect, respond to and even adapt to 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 us. However, 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 rudimentary form of awareness just as they also certainly have some rudimentary higher cognitive abilities.

To establish experimentally if any non-human species is capable of conscious awareness, we need to first determine what particularly distinguishes awareness from simple stimulus-response behaviour. Many 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). These range from being conscious of sensory cues from the environment in an on-line mode, to being able to consciously plan actions through calling up past memories, to being aware of self and the impact of one's thoughts, actions and experiences on both self and others. All these levels of consciousness bring with them the immediate potential capacity to experience subjective emotions, whether they be suffering or happiness. Thus, at this stage in dealing with non-human animals, the first critical problem is to determine experimentally whether they are capable of conscious awareness at all, since that proof in itself would justify concern for their welfare.

Some complex behaviours, eg self-recognition, social communication, individual recognition of conspecifics, deceit and empathy, and complex learning (particularly the application of rules to novel problems and performing tasks such as delayed matching or non-matching to sample which require an individual to form a mental image of the training stimulus) are highly suggestive of consciousness (Kendrick 1997). 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).

The most tractable area for research in this area is the ability to form and use mental images to guide behaviour. While this capacity by itself does not necessarily imply consciousness, it is one of the important component parts. One way forward in trying to establish the presence and use of mental imagery in non-human mammals is to combine behavioural assessments (which are often open to the problems of interpretation) with a consideration of how an animal's brain is organized 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 & Koch 1990).

Recent advances in functional brain imaging techniques using magnetic resonance imaging and positron emission tomography 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 as or different from those which are active when an individual forms a mental image of the objects.

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, 1997; Koch & Braun 1996; Farah & Feinberg 1997). There is not, of course, complete overlap, as illustrated by the phenomenon of 'blindsight' in humans where brain-damaged patients can still respond appropriately to objects without actually being aware of them (Milner & Goodale 1995; Farah & Feinberg 1997; Kentridge *et al* 1999). In some cases it has even been claimed that

visual imagery involves the primary visual cortex (Le Bihan *et al* 1993; Kosslyn *et al* 1995) although others have disputed this (Crick & Koch 1995).

In general, imaging studies in humans, and supportive electrophysiological experiments in monkeys, have indicated 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 & Haxby 1994; Milner & Goodale 1995; Koch & 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 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 potentially be consciously aware. One of the most important areas to focus on in this respect is social recognition and, in particular, recognition using visual cues from the face. This is the main form of social recognition in humans and we are extremely adept at forming mental images of faces. Face recognition also involves a specialized form of neural encoding by the brain within the 'ventral' processing stream. We will examine the case that sheep, like humans, have the same specialized behavioural abilities and neural processing for face recognition together with evidence for whether they can form and use mental imagery for faces. We will also examine examples of where face stimuli do, or do not, evoke parallel activation of brain areas associated with control of behavioural or emotional responses.

### ***Human face recognition***

For humans, individual recognition is clearly mainly guided by visual cues from the face, under normal circumstances, and we are capable of recognizing many hundreds, if not thousands, of people this way. To achieve this, the brain has evolved a specialist neural system for processing visual cues from faces that is different from, and distinct from, that used for most other classes of object. Behavioural evidence has confirmed that we recognize faces in a special way compared to other objects. Thus, unlike other objects and landscapes, we have difficulty in recognizing faces when they are upside down (Yin 1969; Ellis & Shepherd 1975; Wright & Roberts 1996). For familiar faces, we use highly sophisticated cues from the configuration of internal features of the faces (eyes, nose, mouth, etc) to aid recognition (Ellis *et al* 1979; Young *et al* 1985; Rhodes 1993). For recognition, we also make more use of visual cues from the part of the face that appears in our left visual field than we do of those appearing in the right (Levy *et al* 1972, 1983; Overman & Doty 1982). The right side of the brain primarily processes cues from the left part of the visual field since visual information crosses to the opposite side of the brain in the optic nerves.

The main features of this system are that it involves regions in the ventral temporal lobe of the brain (parahippocampal gyrus and fusiform region) particularly in the right brain hemisphere (Sergent & Signoret 1992; Sergent *et al* 1992; Kanwisher *et al* 1996, 1997; McCarthy *et al* 1997). This is in the ventral visual brain processing stream associated with the identification and conscious perception of objects, and functional imaging studies in humans have demonstrated that they are similarly activated during actual perception of faces and when individuals form mental images of them (Kanwisher *et al* 1996, 1997). The neuropsychology literature has also confirmed that damage to these brain regions can lead to

prosopagnosia (difficulty in recognizing people from their faces) without significant visual agnosia for other classes of objects (Sergent & Signoret 1992; Farah 1995; Schweinberger *et al* 1995; Farah & Feinberg 1997). While there is strong evidence for overlap in the neural substrates controlling recognition of faces and conscious perception/mental images of them, they are dissociable. For example, prosopagnosics can be shown to have some covert face recognition skills even though they are not aware of them (Schweinberger *et al* 1995).

Evidence is now accumulating which indicates that this specialist system in humans may not be entirely face-specific and can be used for recognition of non-human faces, or even non-face objects (Diamond & Carey 1986; Gauthier & Tarr 1997; Gauthier *et al* 1999, 2000) where considerable expertise has been acquired. However, there is little doubt that it is a system that is essential for conscious perception and mental imagery of faces. Thus, if another animal species can be shown to exhibit similar specializations in face recognition abilities, and neural processes underlying them, then this would strongly indicate a capacity for their being able to consciously perceive faces and form associated mental imagery.

***Do sheep recognize each other using facial cues?***

We have clearly established, using a Y-choice maze apparatus, that sheep can distinguish between pictures of faces of their own species and other species, between different sheep breeds, between males and females of their own species and between individual females or males of their same breed (Kendrick *et al* 1995, 1996; Kendrick 1998; Peirce *et al* 2000). While individual recognition between breed members of equal social importance requires the use of food reward paradigms, we have also shown that sheep will readily distinguish between faces of socially familiar and unfamiliar animals or between different species or breeds without any training and where the reward is simply to gain access to the individual whose face they have chosen (Kendrick *et al* 1995). They will also distinguish between familiar and unfamiliar humans in the same way. This shows that the animals must use face recognition to distinguish between individuals in their normal lives, and rules out the possibility that we have merely trained them to develop skills for using facial cues. This conclusion is further supported by our findings that in most cases sheep will learn to distinguish between pairs of faces to obtain a food reward in less than 40 trials (less if the faces are of socially familiar individuals) and are actually better at this than learning to discriminate between simple geometric symbols (Kendrick *et al* 1996).

***How many sheep can they recognize and for how long do they remember them?***

While it is extremely difficult to provide an accurate assessment of how many different individuals a sheep can recognize at any one time, we know that it is at least 50. This is because they are capable of being able to discriminate simultaneously between 25 different pairs of sheep faces at any one time where one face of each pair is associated with a food reward. They are also capable of using cues from the configurations of the internal features of faces (eyes, nose, mouth, etc) from any member of an established flock of 50 individuals. We have previously shown that sheep can only use such internal cues effectively when recognizing socially familiar individuals (Peirce *et al* 2000).

Retention of multiple learned face discriminations (25 different face pairs) in a choice maze is also retained significantly above chance performance for periods in excess of 2 years. Furthermore, evidence from cross-fostering studies between sheep and goats has provided evidence for a potential life-long impact of the mother-offspring bond on offspring attraction to faces that resemble that of the mother (Kendrick *et al* 1998). Anecdotal field evidence for long-term kin recognition may also involve face recognition. Thus, the animals

have a remarkable face recognition memory capacity which raises the possibility that they might be able to 'think' about individuals for considerable periods after they have been removed from the flock.

***Do sheep have specialized neural systems for face recognition?***

We originally found in electrophysiological recording experiments that sheep, like monkeys, have neural populations in their temporal cortex which appear to respond selectively to faces as opposed to other objects (Kendrick & Baldwin 1987; Kendrick 1990, 1991; Peirce 2000). Furthermore, some of these cells respond highly selectively to a small number of familiar individuals. Sometimes, responses can only be evoked to the face of a single familiar individual. We have also used molecular markers of neural activation in the brain to determine which regions process faces. These have confirmed involvement of the temporal cortex as well as other regions, such as the frontal cortex and amygdala, also thought to be involved in face recognition in primates (Ohkura *et al* 1997; Broad *et al* 2000). These studies have also confirmed behavioural observations that the right brain hemisphere is more actively involved in face discrimination than the left, with only the right temporal cortex being significantly activated (Broad *et al* 2000).

***Is there evidence for links between areas controlling face recognition in the brain and those involved in making behavioural and emotional responses to them?***

An important question is how areas of the brain specialized for processing faces link with those mediating behavioural and emotional responses. In particular, can we find any evidence for dissociations, in terms of regional activation patterns, under circumstances where the sheep is, or is not, interested in the individuals it perceives? Such dissociations might reflect situations where the sheep are, or are not, consciously aware of the face stimuli they are viewing.

Female sheep mainly show interest in males when they are sexually receptive towards them and will only choose to approach pictures of male faces at this time (Kendrick *et al* 1995). We have shown that, even controlling for the amount of time that a female looks at a male, the brain regions controlling her recognition of faces and those controlling her behavioural responses to him and associated reward pathways are only strongly activated when he is of interest to her sexually (Ohkura *et al* 1997). Thus, there is extensive activation of primary sensory cortical areas, association cortex (including strong activation of the area of temporal cortex associated with face recognition), limbic system and nucleus accumbens. During anoestrus, when the female is not attracted to male cues, the only measurable change is a small activation in the temporal cortex when she interacts with him and there is certainly no corresponding activation of cortical limbic and hypothalamic regions controlling her emotional and behavioural responses, or of reward centres such as the nucleus accumbens. Indeed, it is almost as if a lack of interest, and presumably attention, to his presence could be described as 'in sight but out of mind', and might therefore be similar to covert (unconscious), compared with overt (conscious), processing of sensory cues in humans! Our results also have close parallels with human brain imaging experiments showing that covert recognition of faces produces a reduced activation of the fusiform face area of the brain compared to overt recognition (Wojciulik *et al* 1998).

We have also obtained *in vivo* neurochemical evidence to support this from the hypothalamus where it was confirmed that neurotransmitter changes associated with the making of a sexual response only occurred during oestrus in response to pictures of a male's



face. Also, exposure to the face of a preferred male at this time had a significantly greater impact than the sight of one that was less preferred (Fabre-Nys *et al* 1997).

When sheep discriminate between face pictures of sheep and humans, activation of the area of the right temporal cortex occurs under conditions where the sheep can discriminate well between the faces. However, corresponding activation of limbic regions such as the amygdala and hippocampus only occurs when the animals are prepared to make an active choice between them (Broad *et al* 2000). It could therefore again be argued that parallel activation of brain regions associated with face perception and those mediating emotional and behavioural responses only occurs when animals are interested and respond positively to the stimuli being perceived (ie overt 'conscious' recognition).

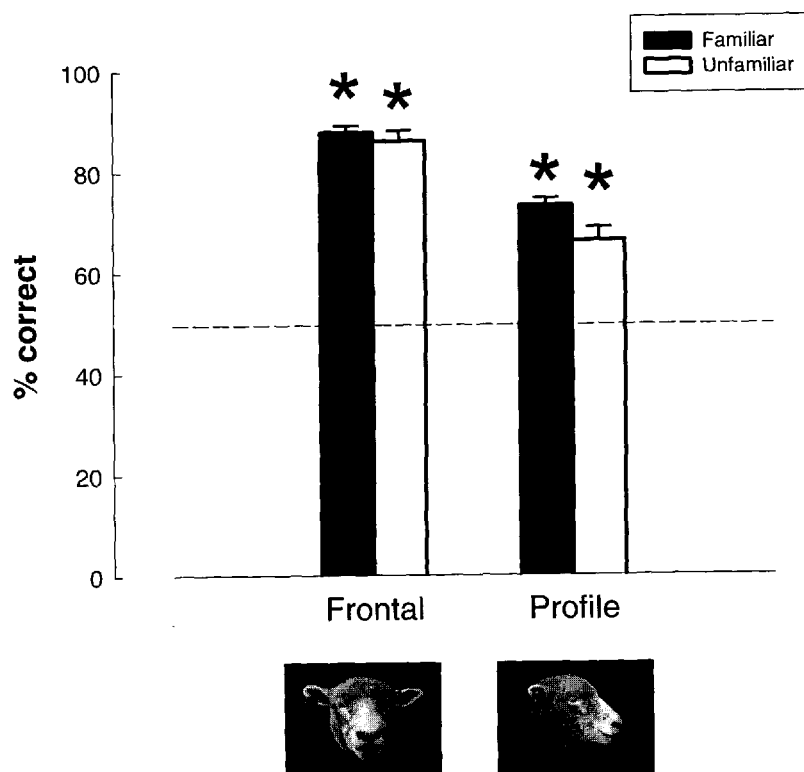
The final evidence of interactions between centres in the sheep brain controlling perception of faces and those mediating behavioural and emotional responses comes from an analysis of coding strategies employed by cells in the temporal cortex that respond to faces. These cells respond to face stimuli in around 100ms, ie before the animal can make any form of voluntary motor response (Kendrick & Baldwin 1987; Kendrick 1990, 1991, 1994; Peirce 2000). However, rather than encoding faces on the basis of their physical similarities, they clearly encode them on the basis of similarity of behavioural or emotional significance. Thus, we originally found that faces with horns were specifically encoded by one population of cells, another population encoded faces of animals of the same sheep breed, and particularly socially familiar individuals, and a final population encoded faces of humans and dogs. This last category, in particular, makes this point most clearly since dog and human faces do not share many similar physical characteristics, but for sheep they both represent classes of potentially threatening stimuli. Recent findings have further supported this conclusion, where we have consistently found cells which can respond to faces both of socially familiar sheep and of one specific human stockman who had had a very long and positive relationship with the sheep under his care (other human faces were not effective; Peirce 2000). Thus, these cells would appear to be classifying any individual engendering some form of positive social response (whether sheep or human or presumably any other species).

The face-sensitive cells in the temporal cortex are assumed to have extensive interconnections with other cortical and limbic structures mediating behavioural and emotional responses and thus one has to assume that their coding strategies are shaped by feedback pathways from these latter structures. Thus this represents further evidence for formative interactions between face-processing regions of the brain and those mediating an animal's emotional response to them.

#### ***Can sheep form and use mental images of faces?***

We have so far only some very preliminary evidence to indicate that sheep can indeed form and use mental images of faces. The first experiments we carried out addressed the issue of whether sheep could recognize different views of faces to that they were trained on in a choice Y-maze. Thus we asked the question whether they could immediately recognize profile views of the sheep faces having been trained only using frontal views of them, or *vice versa*. While some of the same facial features are present in both frontal and profile views, their orientation, and therefore appearance, are very different. In all cases, face images were viewed against a neutral uniform black background to eliminate any common peripheral visual cues. The ability to determine that a particular profile view belongs to the same animal viewed from the front should therefore involve some capacity to mentally rotate the face image. Sheep can indeed perform this task with both familiar and unfamiliar

sheep faces, and even with human faces (Figure 1). There are also cells within the temporal cortex which respond equivalently to frontal and profiled views of faces (Peirce 2000) and these presumably assist in the process of mental rotation. While we cannot entirely rule out the ability of the animals to use some sophisticated form of stimulus generalization to determine that a profile view of a face belongs to the same individual that has previously been viewed only from the front (or *vice versa*), it seems unlikely that this is happening. The main reason for supposing this is that features that are common to both frontal and profile views of faces look very different in the two cases due to being turned through 90°. One could also argue that if they were able to use stimulus generalization in this context then they should also be able to recognize inverted views of the same face, whereas they cannot.



**Figure 1** Histograms show mean  $\pm$  SEM per cent correct responses made by sheep in a two choice maze to pairs of faces (one of which is associated with a food reward) initially presented in frontal view and then for 10 trials presented in profile. Results show that the animals still perform significantly above chance for the novel profile view irrespective of whether the faces used are of socially familiar or unfamiliar individuals. \*  $P < 0.05$  vs chance (50%; data are from 10 animals). The animals are unable to do better than chance for learning a novel discrimination based on profile views presented for only 10 trials.

A second task we have developed which should require the use of mental imagery is matching to sample using face images. In this task, the animal views a single face and, after a

variable delay, is shown two faces, one of which is the face shown originally. The animal is required to identify the face it has just seen (matching to sample), or alternatively the face that it has not previously seen (non-matching to sample) in order to obtain a food reward. This is a common working memory task in human experimental psychology and successful performance is generally thought to involve the individual having the capacity to form and hold a mental image of the training stimulus up until the point where the recognition test is presented. As such, it is a very difficult task and not one that is easily demonstrated (in terms of visual object recognition) in non-primate animals. However, ability to perform this task using symbols has been demonstrated in goats (Soltysik & Baldwin 1972). Our initial evidence in sheep has so far shown that they are able to do this (70–80% correct choices) with at least some sheep faces and can even cope with short delays (10–15 s). However, further work is needed to assess their overall abilities more precisely and considerable amounts of training are required for them to acquire this task.

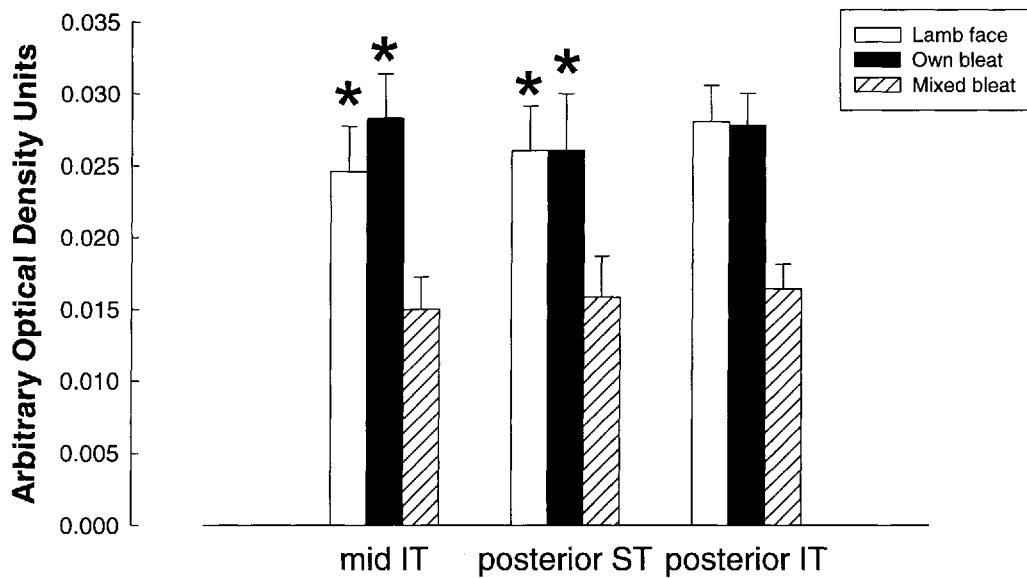
***Do stimuli designed to evoke mental images of faces in sheep activate face-processing regions of the brain?***

So far we have made two approaches to addressing this question. The first has been to establish whether non-visual cues can evoke activation of regions of the temporal and frontal cortices that respond to visual cues from faces. The model chosen was maternal ewes responding to the bleats of their lambs after a period of separation. This was chosen since, by 1 month post-partum, ewes readily recognize their lambs from their faces and it was felt that hearing the lamb's bleat alone after a period of separation might evoke a visual mental image of its face. Previous electrophysiological studies had also failed to find any evidence that face-sensitive neurones in the temporal cortex could respond to auditory stimuli. Under these circumstances, it was found that bleats did indeed produce similar levels of activation (as evidenced by quantifying altered messenger RNA expression of the immediate early gene, *c-fos*, which is widely used as a neuroanatomical marker of increased neural activity in the brain – see Broad *et al* [2000]) in the temporal and frontal cortices as following exposure to pictures of the lambs' faces. As a control, it was shown that exposing the ewes to the same lamb bleat vocalizations but reorganized in a random sequence failed to produce the same level of activation (Figure 2).

The second method we have started to employ is the use of digitized video sequences as stimuli while recording from cells in the temporal cortex that are responsive to the faces of specific familiar individuals. Recent work has shown that a proportion of face-sensitive cells in this region responds selectively to only one or two socially familiar individuals. We have therefore constructed video sequences which are shot from a sheep's eye level and which eventually reveal the presence of the specific socially familiar individual in its home pen. The animals are repeatedly exposed to this video sequence while recordings are made from cells that respond selectively to pictures of the sheep's face. Randomly interposed in these repeated video sequences are similar sequences which, when they finally reveal the home pen, reveal it as no longer containing the familiar individual. Initial work has identified small numbers of cells that respond equivalently to the situation where the sheep is revealed in its pen and when it is not. This could be regarded as some form of simple conditioning, although we have previously found it difficult to demonstrate conditioned responses from face-sensitive neurones using visual objects or symbols paired with faces. However, interestingly, after many repetitions of the video sequences, cell responses can often be seen at key stages in them which could be considered to most strongly indicate the imminent appearance of the familiar sheep (ie when the sequence moves to the entrance of the room



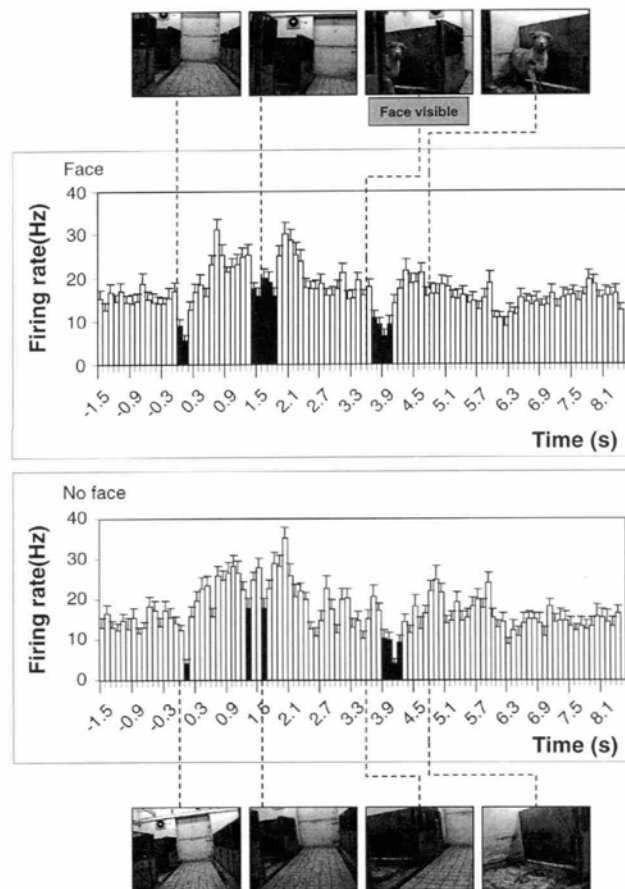
containing the sheep and when it moves in to show a first glimpse of its pen through an open door – Figure 3). Thus, from having only responded to pictures of a particular sheep's face (and not to pictures of empty sheep pens), video sequences which are highly suggestive of the imminent appearance of that sheep can evoke neural responses irrespective of whether the sheep is actually viewed or not. Clearly other paradigms that are designed to evoke mental images of specific individuals, such as their being obviously hidden behind screens or in the delay period during a matching to sample task will be needed to provide more supporting evidence.



**Figure 2** Histograms show mean  $\pm$  SEM levels of *c-fos* mRNA expression (used as a molecular marker of increased neural activation) in regions of the temporal cortex in sheep. Data show equivalent levels of expression by maternal ewes in response to pictures of lambs' faces or exposure to audio tapes of their lamb's bleats. There is significantly less effect of exposure to a control presenting randomized sequence of the lamb's bleats (mid IT = mid inferior temporal cortex; ST = superior temporal cortex). \*  $P < 0.05$  vs mixed bleat.

### Conclusions

There is therefore a large amount of evidence for remarkably similar behavioural and neural specializations for face recognition in sheep to those found in humans. While more work is required to provide evidence that the face recognition system in the sheep brain is also capable of generating mental images of faces, as it is in humans, preliminary data are strongly indicative of this. The fact that face recognition memory is so fast and durable does beg the question that it has evolved to allow the animals to remember large numbers of individuals and potentially even 'think' about them in their absence. The fact that parallel activation of limbic and frontal cortical regions in response to faces occurs under



**Figure 3**

Histograms show mean  $\pm$  SEM changes in firing rate of a cell in the left temporal cortex during presentation of a 6s video sequence which either shows the presence of a familiar sheep (top) or does not (bottom). This cell's primary response to the familiar sheep face is inhibition although the period of inhibition is often followed by a rebound excitation. The histograms represent 20 different presentations of the same films (which start at time 0 and finish after 6s) and show that the cell responds both during the actual appearance of the individual and at the same time in the film where the individual should have appeared but does not. However, in both video sequences the cell also responds at the beginning of the film sequence and at the point where the open door of the pen containing the stimulus animal is first shown. Statistically significant initial inhibition in firing rate is indicated by black bars in the histograms (*t*-test;  $P < 0.01$ ). There is a close correspondence in response profiles in the two film sequences, although in the film where the sheep is absent a slight increase in response latency occurs. This cell failed to respond to any non-face image presented, or to other sheep of the same breed as the familiar animal used in the film sequence, or to videos of different environments not normally associated with the presence of sheep.

circumstances when the animals show overt interest in them might also indicate that when this occurs they are consciously aware of the stimuli and their actions towards them.

### ***Animal welfare implications***

This work showing sophisticated use of facial cues by sheep to recognize one another, together with evidence supporting the possibility that they may be able to form and use mental images of faces, implies a level of cognitive and social complexity not commonly ascribed to this species. The welfare implications are therefore to take into consideration providing sheep with stable social environments and, from a pragmatic point of view, to make sure that their vision is not impeded by lack of appropriate husbandry (ie cutting fleece or trimming horns).

### **Acknowledgements**

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