Human face recognition in sheep: lack of configurational coding and right hemisphere advantage


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Received 5 October 2000; received in revised form 12 February 2001; accepted 22 February 2001

Abstract

Face recognition in sheep is qualitatively similar to that in humans in terms of its left visual field bias, and the effects of expertise and configurational coding. The current study was designed to determine whether such effects are species specific by investigating the case of sheep recognising humans. It was found that the sheep could identify human faces and while they showed a small inversion-induced decline in discriminatory performance, this was significantly less than seen with sheep faces. In other aspects, there were qualitative differences with human face recognition compared with conspecific recognition. In contrast with sheep faces there was no left visual field advantage in the recognition of human faces and the internal features were not used at all as visual cues. The data suggest that these sheep, whilst being extensively exposed to interactions with humans, were unable to identify them with all the same ‘expert’ methods as were used to discriminate other sheep. This suggests that different neural systems may, to some extent, be used for recognition of sheep as opposed to human faces. The relative contribution to differential neural processing of the faces of the different species and the role of expertise are discussed. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Asymmetry; Hemispheric lateralisation; Chimeric; Face processing; Expertise; Inversion

1. Introduction

Sheep may at first glance appear a surprising choice for an animal model of perceptual processes. They do however have very good vision (acuity estimated at 3–4'; Piggins, 1992) in their binocular field (which is roughly 40–60°) and are a highly sociable animals. In the field, there is considerable evidence for their social requirement to identify both categories of individuals (they show preferences for maintaining social proximity with members of their own species and breed) and also specific individuals (they form individual consortships and need to be able to identify specific individuals; they also selectively bond with their offspring and need to recognise them) (Kendrick, 1994; Kendrick et al., 1995, 1996). For sheep, as humans, the area of the body showing the greatest
degree of heterogeneity is the face. Thus, the ability to use visual cues to discriminate between individual faces might be extremely useful. As a result, they have been studied for some time at behavioural (Kendrick et al., 1995, 1996; Peirce et al., 2000) and electrophysiological (Kendrick and Baldwin, 1987; Kendrick, 1994) levels for their ability to recognise faces.

The use of the Y-maze (two-way conditioned discriminations) with Clun Forest and Dalesbred sheep has already shown that they are capable of discriminating between various photographically represented objects such as sheep versus dog, human and goat faces (Kendrick et al., 1995). They could also distinguish visually between different breeds of sheep, between genders within their own breed and even between individual ewes (Kendrick et al., 1996). Furthermore, effects of familiarity were found with the faces of sheep of the same breed (where the stimulus face came from the same flock as the subject), with associations with food rewards being learned more quickly than those using unfamiliar sheep (Kendrick et al., 1996).

In humans, it has been suggested that expert mechanisms might exist for the recognition of faces. When faces are inverted they become very hard to identify, much more so than other everyday objects (Yin, 1969). This is mainly due to the use of configurational cues, which are used more in faces than in the recognition of other objects. Other studies have shown that we make greater use of internal features, which contain more configurational cues, to recognise faces that are very familiar (Ellis et al., 1979; Young et al., 1985). The use of feature configuration cues is also thought to be related to the disproportionate right hemisphere occipitotemporal cortex activation during face recognition, which has been noted by various neuro-imaging methods such as PET and fMRI (e.g. Sergent et al., 1992; McCarthy et al., 1997). This right hemisphere bias appears to cause a perceptual bias in the visual hemifield that is attended to during face recognition studies. The left visual hemifield (which projects predominantly to the right hemisphere of the brain) has been shown to be more crucial to the recognition of faces in humans by a variety of studies utilising tachistoscopic (e.g. Ellis and Shepherd, 1975) as well as free-viewing methods (Wolff, 1933; Levy et al., 1983; Burt and Perrett, 1997). However, the interdependence of the effects of expertise, left hemifield bias and configuration has been difficult to show conclusively (e.g. Rhodes, 1993).

In sheep, the interaction between familiarity, hemifield bias and the use of internal features has also been studied explicitly (Peirce et al., 2000). It appears that sheep faces are recognised more by the left visual field (when stimuli are simply half-faces or are mirrored down the centre-line) and this effect is stronger for familiar faces (as measured with chimeric face stimuli). In addition, faces that are more familiar are recognised partially by the ‘internal’ features (nose, eyes...) whereas unfamiliar stimuli are seemingly recognised purely from the ‘external’ cues (fleece, ears...).

Another study in sheep actually measured the neuroanatomical areas involved in face recognition by measuring c-fos expression (an immediate-early gene used as a marker of neural activation) during the face discrimination task. The experiment showed there was a strong c-fos activation in the temporal cortex, especially in the right hemisphere, when faces were presented upright (Broad et al., 2000). When faces were inverted recognition was impaired and there was no longer evidence for enhanced activation in the right temporal cortex. The findings suggest that the systems involved in recognition of face stimuli are predominantly located in the right hemisphere of the sheep brain, supporting the behavioural data described by Peirce et al. (2000).

What is uncertain is whether any other visual stimuli are recognised by the same cues as these sheep faces, which would imply the involvement of similar neural mechanisms. In humans it has been found that simply by providing a great deal of contact with a stimulus category and frequent attempts to discriminate exemplars, expertise in recognition can develop which is quali-
tatively similar to recognition of faces (Diamond and Carey, 1986; Bruyer and Crispeels, 1992). Thus faces are only special through experience. The effect is also observed in naïve subjects who are trained to recognise novel, artificial visual objects called ‘Greebles’ (Gauthier and Tarr, 1997). Furthermore, areas of the brain normally associated with the recognition of faces (such as the Fusiform Face Area, FFA; Kanwisher et al., 1997) are activated when we view these objects after the training procedure (Gauthier et al., 1999, 2000). It is possible that spatially distinct neural populations within the FFA may encode different types of familiar faces or objects since some humans with stroke-induced prosopagnosia cannot learn to recognise human faces but can nevertheless learn to recognise animal faces (McNeil and Warrington, 1993).

To determine whether experience is sufficient for the development of the face processing mechanisms observed when sheep discriminate conspecifics, we have tested their abilities to recognise human faces. Sheep have no strong evolutionary pressure to discriminate between humans, but by exposing them to extensive interactions and close contact with a number of humans, we attempted to change this. Previous studies have found that sheep are capable of discriminating humans from sheep using photographs of faces (Kendrick et al., 1995) and that discriminations between individual humans can occur in the context of the animal’s home pen (Davis et al., 1998). In this latter case, however, the recognition was not purely visual but very likely included an olfactory component. Thus, the first goal of the current study was to see whether sheep constantly exposed to a number of different humans could learn to discriminate between individual human faces. The second goal was to determine how similar such recognition was to the expert mechanisms of face recognition previously observed when sheep were viewing familiar sheep. That is, the degree to which the left visual field and internal features were used to identify the human stimuli and the extent to which inversion impaired discriminatory performance.

2. Method

2.1. Subjects

The animals used were 10 adult polled Dorset ewes (the same individuals used by Peirce et al., 2000 to study sheep recognising sheep faces). This is a hornless breed with high facial homogeneity (predominantly white). They had been extensively trained in the Y-maze procedure, whereby they were given a food reward for choosing a target stimulus, and were habituated to the maze environment and the experimenters. They were kept amongst a flock of 30–50 sheep. The humans in frequent contact (2–3 h per day) with the animals included roughly 10 individuals such as animal care assistants and experimenters over a period of 3 years. Food (grass or hay) and water was provided ad libitum throughout the study.

2.2. Stimuli

The stimuli used for training and testing exactly mimicked those used by Peirce et al. (2000) except that they were based on human faces. They were created from pictures of faces taken using a regular 35 mm camera and scanned at high resolution into a digital format. The faces were chosen as the four humans with most frequent contact with the sheep and four unfamiliar faces, matched roughly for age and general visual appearance. The background of the photographs was edited out on a Pentium PC computer, leaving just a head on a black screen. The images were then printed in full colour onto photographic slides which were back-projected onto a screen in the Y-maze such that the face was seen at roughly life-size. From the training stimuli, the following manipulations were made.

2.2.1. To investigate visual field bias (Fig. 1)

2.2.1.1. Hemifield. Half of the face was obscured by a black mask. Similar to stimuli used by Dittrich (1994).

2.2.1.2. Hemifield mirrored. Half of the face was
mirrored onto the other half (also referred to as left–left/right–right faces). Similar to those used by Overman and Doty (1982).

Fig. 1. Examples of stimuli to ascertain visual field bias 1: (a) a pair of training stimuli; (b) left hemifaces; (c) left–left mirrored faces; (d) chimeric faces. Actual stimuli were in full colour.

Fig. 2. Examples of stimuli to ascertain use of internal features: (a) internal features only; (b) external features only; (c) scrambled features; (d) swapped-feature stimuli.

2.2.1.3. **Hemifield chimeric.** The traditional chimeric face stimuli (Levy et al., 1983; Morris and Hopkins, 1993) where the left and right of two separate faces (in this case the rewarded and non-rewarded) are combined to form one.
2.2.2. To investigate use of internal vs. external features (Fig. 2)

2.2.2.1. Internal only. The external features of the face were covered using a black oval mask.

2.2.2.2. External only. The internal features were covered with a skin texture leaving only the external face shape visible.

2.2.2.3. Scrambled. The internal features of the face were present but in a new spatial configuration. All stimuli were given the same overall configuration (mouth moved to top left of face etc...) and the edges of the features were then smoothed into the skin texture.

2.2.2.4. Swapped features. The inner oval for the target face was swapped with the same area of the non-rewarded stimulus to create a chimeric-type stimulus.

2.2.3. To investigate inversion effects

Performance on discriminating the same human face pairs as used in the above experiments was re-tested with normal frontal views presented inverted. Comparisons were made with performance by the same animals on discriminating between pairs of faces of sheep of the same breed (five pairs of socially familiar individuals of the same breed and five pairs of socially unfamiliar individuals of the same breed).

2.3. Procedure

The Y-maze apparatus and protocol has been described elsewhere (Kendrick et al., 1995; Peirce et al., 2000) and differed very little in this study. The animal entered a start box from where it could see to the ends of the two arms of a Y-maze. Here, two stimuli were projected on back-projection screens located next to two exit doors. As the animal entered the body of the Y-maze, it broke a light beam, which triggered a timer. By approaching one of the pictures a second light beam was triggered (1.5 m from the first) which stopped the timer and opened the door next to the relevant stimulus. The sheep then exited into a goal pen where an experimenter was waiting with either an empty or full bucket of food (sheep nuts). After receiving a mouthful of food the animal was ushered into a further holding pen to await the start of the next trial. The position of the target stimulus was randomised across trials. Each trial (of all 10 animals) took 3–5 min to complete and 20 trials were performed on each day.

Whilst it is not possible to record fixation position within the Y-maze environment it is expected that the animals fixate centrally, or at least scan evenly across the stimuli, during the presentation of training stimuli. In general, the time from entrance into the start box until breaking the exit light beam was $< 3$ s. Of this on average 1.7–2 s was required to travel between the start and stop light beams. With the animals usually orienting towards the face picture that they would ultimately chose virtually from the moment they actually entered the choice maze itself, and broke the start light beam, it is likely that actual discrimination choice was effected in many cases after scanning the two pictures for only 1–2 s.

Stimuli were sorted into pairs of faces (two pairs of familiar and two pairs of unfamiliar) and the sheep were trained on one pair at a time where one of the faces was consistently associated with a food reward. Due to the fact that the normal animal handlers include one female, one pair of each face type (familiar and unfamiliar) included a male/female pairing as in the example stimuli shown (Figs. 1 and 2), with the other pair being both male faces. The effects of the mixed/same-gender stimuli were included as a further factor in the statistical analysis of the results to rule it out as a confounding variable.

The animals all received the same number of discrimination trials in the study but responses to manipulated face stimuli did not start until all the animals had achieved 80% accuracy or above (the best subjects can average around 90–95% accuracy in this and other Y-maze tasks). The test period then involved 1 day of 20 trials for each stimulus type (including others not described here) where the same two faces were used but in their degraded format. For instance, 1 day the animals might be tested with left hemifield faces...
for 20 trials and on the next day the stimuli might be internal features of the faces etc... The order of test stimuli was randomised between stimulus pairs. When all test stimuli had been run for one stimulus pair the next training set was started. Using this approach, the animals had exactly the same amount of experience of the different types of manipulated faces. The amount of exposure to tasks requiring the animals to show if they could discriminate cues from the left as opposed to the right sides of the face and internal compared with external face features was also completely counterbalanced.

During testing, the animals were still rewarded for choosing the correct face. The only exception to the general protocol was when the chimeric stimulus set (Fig. 1d) and swapped feature stimuli (Fig. 2d) were used. In these cases both stimuli contained information from the original rewarded face. Hence, either was a correct choice and the animal was always rewarded.

3. Results

For the human face discriminations sheep required 27.8 ± 5.7 (mean ± sem) trials to reach the 80% correct criterion for familiar faces and 74.6 ± 13.7 trials for unfamiliar faces. This contrasted with the same animals requiring 35.3 ± 7.5 trials for familiar sheep faces and 63 ± 9.7 trials for unfamiliar ones. Analysis of variance (ANOVA) showed that there was a significant variation in the number of trials required (F = 9.76; d.f. = 3.27; P < 0.001) and Tukey’s post-hoc test showed that this was due to significantly more trials being required to learn unfamiliar human (P < 0.001) or sheep discriminations (P < 0.05) compared with familiar ones. There was however no difference between the number of trials taken to learn to discriminate familiar or unfamiliar sheep faces compared with familiar or unfamiliar human faces. For response times there was again a significant variation across the human and sheep face discrimination conditions (F = 8.226; d.f. = 3.27; P = 0.0005). Tukey’s test revealed that this was due to response times being longer for unfamiliar humans (mean ± sem = 2.14 ± 0.21 s) compared with familiar humans (1.82 ± 0.13 s; P < 0.05) or familiar sheep (1.62 ± 0.12 s; P < 0.001). Response times for unfamiliar sheep did not differ significantly from any of the other discriminations (1.87 ± 0.13 s; P > 0.05 in all cases).

3.1. Visual field bias

All data were analysed statistically with the two gender groups (same sex stimuli and mixed sex stimuli) separate, the effects of which were also of interest. In the interest of graphical simplicity however, these were combined to produce the graphs which simply compare familiarity and hemifield biases (Fig. 3).

A 3-way (Visual field × Familiarity × Stimulus gender) Analysis of Variance (ANOVA) for hemifield stimuli showed a main effect of stimulus gender (F = 5.72; d.f. = 1.79; P = 0.019) and of familiarity (F = 7.44; d.f. = 1.79; P = 0.008), with opposite-gender stimuli and familiar faces being discriminated more accurately. There was no effect of hemifield (F = 1.69; d.f. = 1.79; P > 0.05) nor any interactions between the factors. In terms of reaction times there were no significant effects at all in the hemiface data.

With mirrored faces (Fig. 3b), the pattern was similar although in this instance there was no main effect of stimulus gender (F = 0.71; d.f. = 1.79; P > 0.05). This left only a significant main effect of familiarity (F = 5.57; d.f. = 1.79; P = 0.021) with familiar faces again being recognised more accurately. For these mirrored stimuli the three-way ANOVA on the response times also showed a main effect of familiarity (F = 4.04; d.f. = 1.79; P = 0.048) with the familiar faces being recognised faster.

For chimeric faces (Fig. 4) there was no significant choice by the sheep towards a particular visual field in the familiar stimuli, by any individual or by the population (choice = 51%, n = 400, P = 0.67 — binomial test). However, for the unfamiliar faces there was a bias towards the right visual field (i.e. opposite to the normal bias), which was significant for one individual and
highly significant for the population (choice = 42%, n = 400, P < 0.001).

3.2. Use of internal features

Again, the gender of stimuli was included as a separate factor for statistical analysis but was not separated in the graphical presentations (Fig. 5) for ease of viewing. Three-factor ANOVA on the face data showed that there was a highly significant difference in recognition accuracy between the stimulus types (internal, external, scrambled features) ($F = 19.92$; d.f. = 2,119; $P = 0.001$). The factors of familiarity and stimulus gender yielded no significant differences. The stimulus gender interacted significantly with both the familiarity effect ($F = 4.77$; d.f. = 1,119; $P = 0.031$) and, more importantly, with the above mentioned effect of stimulus type ($F = 7.25$; d.f. = 2,119; $P = 0.001$). It appears that this was caused by an increased use of external over internal features when the stimuli were of opposite sex, presumably due to the hair looking so different. In terms of response time the gender/external-feature interaction was also the only significant result for these stimuli ($F = 3.28$; d.f. = 2, 119; $P = 0.041$), which showed that the mixed-sex discrimination was performed not

![Graphical Representation]

Fig. 3. Results from: (a) hemiface; and (b) mirrored hemiface stimuli. In both stimulus sets there was a significant main effect of familiarity (*$P < 0.05$), with familiar faces being recognised more accurately (and also faster in the case of mirrored face stimuli). No main effects of hemifield were observed, or any interaction between hemifield and familiarity. Hashed line represents chance performance.
only more accurately than any other but also more quickly (Fig. 5a).

For swapped-feature stimuli (Fig. 5b), familiar faces were chosen a disproportionate amount of the time by the external features by all individuals and the population (choice = 82%, n = 400, P < 0.001 — binomial test). For unfamiliar faces, all except one subject showed preference for the external features and this was also significant over the population (72%, n = 400, P < 0.001). A t-test confirmed that the effect of the external features was stronger for familiars (t = 2.96, d.f. = 9, P = 0.016). For these the increased choice time was also approaching significance (t = 2.17, d.f. = 9, P = 0.057).

3.3. Effects of inversion

Again, for human faces, the gender of stimuli was included as a separate factor for statistical analysis but was not separated in the graphical presentations (Fig. 6a) for ease of viewing. Three-factor ANOVA on the data (Inversion × Familiarity × Gender) showed that there was a significant difference between accurate discrimination of upright and inverted faces (F = 25.8; d.f. = 1,79; P < 0.001), with inversion impairing performance. There was also a main effect of familiarity (F = 6.14; d.f. = 1,79; P = 0.016), with performance being better with familiar faces, but not for gender (F = 0.78; d.f. = 1,79; P = 0.381). There was also a significant interaction between familiarity and gender (F = 11.58; d.f. = 1,79; P < 0.001) and between inversion, familiarity and gender (F = 4.59; d.f. = 1,79; P = 0.036). It appears that this was due to inversion having the strongest effect with familiar and unfamiliar human faces of different sexes and particularly with unfamiliar faces. Indeed, individual t-tests confirmed that significant inversion effects were only achieved with familiar (t = 2.842; d.f. = 9; P = 0.0193) or unfamiliar faces (t = 4.386; d.f. = 9; P = 0.0018) of different genders. With the two same-gender face-pairs inversion just failed to achieve significant effects (P = 0.07 familiar; P = 0.06 unfamiliar). Overall, there were no significant effects of inversion on response times.

The effects of inversion on discrimination of sheep faces are shown in Fig. 6b. For sheep faces a two-factor analysis of variance was carried out (Inversion × Familiarity). This showed that there was a significant difference between accurate discrimination of upright and inverted faces (F = 120.9; d.f. = 1,39; P < 0.001), with inversion impairing performance. As with human faces there was a main effect of familiarity (F = 6.43; d.f. = 1,39; P = 0.016) with performance being better for familiar faces. However, unlike human faces, there was no significant interaction between inversion and familiarity (F = 1.12, d.f. = 1,39; P = 0.297). A further analysis showed that all of the 10 pairs of sheep faces used in the study showed significant inversion effects (t-tests: P < 0.01–P < 0.001 in all cases). No significant effects of inversion on response latencies were seen.

In a final analysis the magnitude of the effect of inversion with both familiar and unfamiliar sheep and human faces was tested by expressing inversion effects as the proportionate change within each animal for inversion performance compared...
Fig. 5. (a) Effects of external only, internal scrambled and internal only stimuli. The accuracy data showed a main effect of stimulus type (**P < 0.001) and this interacted significantly with familiarity (*P < 0.05) due to the differential response in the external feature stimuli; (b) with swapped feature stimuli all except for one animal chose the external features significantly more than internal, regardless of familiarity. A single individual responded at chance (†P > 0.05) for unfamiliar faces, making no choice between internal and external features. A t-test on the RT data showed that there was a trend (P = 0.054) for the unfamiliar faces to be recognised faster than the familiar ones.
Fig. 6. Results showing inversion effects on discrimination of: (a) Human faces; and (b) Sheep faces. In both stimulus sets there was a significant main effect of inversion (human or sheep faces: ***$P < 0.001$) and familiarity (*$P < 0.05$ in both cases). Discrimination of inverted faces was impaired and effects were strongest with unfamiliar faces. The magnitude of the inversion effect was significantly greater with sheep than with human faces (familiar faces — # $P < 0.05$; unfamiliar faces — ### $P < 0.01$). Dashed line represents chance performance. Inversion did not significantly alter response times but response times for normally oriented unfamiliar human faces were significantly longer than those for familiar humans ($P < 0.05$) or sheep ($P < 0.001$).

with that for normal orientation. This revealed that inversion-induced impairments in discriminatory performance were significantly greater for sheep than human faces irrespective of whether faces were familiar ($t = 2.326$; d.f. = 18; $P = 0.0319$) or unfamiliar ($t = 3.08$; d.f. = 18; $P = 0.0064$).

4. Discussion

This study has shown for the first time that sheep are capable of discriminating between pairs of familiar or unfamiliar human faces visually using two-dimensional stimuli. While the speed with which they learned these discriminations and
their response times were similar to those for sheep faces there was little evidence for their being able to use the same expert mechanisms as for sheep faces. As with sheep faces, there was a significant improvement in ability to learn associations with familiar as opposed to unfamiliar human faces. This also indicates that while experience with specific human faces did improve discriminatory performance this nevertheless did not result in the use of the same expert processing mechanisms as for sheep faces. It remains probable however that this is not the only cue that they might use to recognise humans in normal situations or in experiments such as those by Davis et al. (1998). Odour cues, for instance and body shape might both be very important (Kendrick, 1994).

The main aim of the experiment was to ascertain what degree of expertise the sheep might have developed with respect to human faces, in terms of left visual field bias and use of internal features. It appears that their performance in this respect is very different indeed from their recognition of sheep faces. For instance, whilst all three stimulus manipulations showed a left visual field bias when sheep discriminated between the faces of socially familiar sheep, and with hemiface and mirrored face stimuli for socially unfamiliar individuals (Peirce et al., 2000), there was no indication of a similar bias in the same animals with either familiar or unfamiliar human faces. In fact for unfamiliar human faces, there was a slight reverse bias (in favour of the right visual field) when chimeric faces were presented. This suggests that, unlike sheep face stimuli, the human faces may be being processed symmetrically in the sheep brain, or possibly even with a slight bias in favour of the left hemisphere. This latter observation might even be supportive of recent human brain imaging studies showing that while whole faces (which are configururally encoded) strongly activate the right fusiform face area, facial features in isolation (i.e. where no configural cues can be used) activate the left (Rossion et al., 2000).

While the mode of presentation used in this and previous studies (Peirce et al., 2000) did not control for direction of eye gaze, or use tachistoscopic presentation methods to help ensure that visual stimuli were routed to one hemisphere or the other, the speed of both the decision making (1–2 s) and response phases (1.5–2 s) of the task strongly suggests the animals were using optimal attentional and strategies to solve the discriminations. Thus, it is probable that visual field advantages with sheep faces do indeed reflect asymmetric processing of faces by the brain (in support of our previous neuroanatomical study — Broad et al., 2000) whereas the absence of visual field effects with human faces suggests that they are not processed asymmetrically. In humans, left visual field advantages are seen in both free-viewing or controlled presentations of stimuli. In all probability therefore when either humans or sheep are required to recognise familiar types of faces they automatically use this optimal and rapid method for effecting recognition irrespective of how much time is actually allowed.

Since most of the face recognition literature considers the importance of the right hemisphere in face recognition to be in processing the configurational information of the internal features (e.g. Levy et al., 1972; Rhodes, 1993), it might be expected that human face stimuli are processed very much by external or isolated features. In the second part of the study this was found to be just the case. In fact, the most accurately identified stimuli were the scrambled feature faces, which contained the most featural information but no configurational information at all. The next best stimuli in terms of accuracy were the faces with only external features visible, whilst the worst were those with internal features visible. All these stimuli highlight the fact that the internal features were of very little help in discriminating human faces and that their configuration was certainly not important. In contrast, the previous study using sheep faces found that when the stimuli were highly familiar to the subjects, the internal features were an additional useful cue to identity (Peirce et al., 2000).

The use of external features was even more prevalent in discriminations between genders than within male stimuli, probably due to the differences in hairstyles of the stimuli. There was not, however, any interaction between gender and hemifield bias, suggesting that this hair cue was not ultimately the reason for the observed differences in processing.
Inversion-induced impairments in discrimination are particularly marked with faces and this is also interpreted as evidence for strong reliance on configural cues as a result of specialised neural processing of faces. While the sheep in this study did show an overall significant reduction in discriminatory performance with inverted human faces, it was significantly less marked than that seen with sheep faces. It was also restricted to familiar or unfamiliar face pairs of different genders and this might possibly reflect confusion caused, for example, by the somewhat unnatural appearance of some of the external features of the female faces we used (long hair) when they were shown inverted.

However, it should be pointed out that with humans there are also small significant inversion effects with some non-face objects (Yin, 1969; Diamond and Carey, 1986) and we have seen trends in this direction in a previous study in sheep (Kendrick et al., 1996).

Since the sheep used in the Y-maze had a great deal of close visual contact with humans (on average 2–3 h per day for >3 years with at least 10 different individuals — i.e. considerably more than sheep would normally be afforded), it might be expected that they would have developed some capacity for recognising at least familiar humans ‘expertly’, and utilise the same specialised neural substrates employed for ‘expert’ recognition of sheep faces. The fact that this was not the case implies that, for some reason, experience and the need to discriminate (e.g. in order to distinguish between the man who feeds them and passers-by) was not sufficient for the sheep to fully develop expert recognition. It could be argued that expertise did not develop due to the interactions between humans and sheep being more passive than active or the limited number of human face exemplars experienced compared to those of sheep. While these possibilities cannot be entirely ruled out, the sheep in this study did in fact interact quite actively with their handlers as a result of the long periods of daily testing. Their food rewards were always given directly by the humans themselves and the sheep often sought proximity with specific humans and vied for their attention. Also, the sheep used in the study had only had experience of 50–60 different sheep faces during their lives which is not so much greater than the 10 human faces experienced.

A further possibility is that the task of discriminating between the human faces chosen was so easy to solve for the sheep that they did not need to utilise the same expert configural coding mechanisms required for discriminating between sheep faces (i.e. the task of discriminating between highly homogeneous sheep faces might simply have been more difficult and required use of configural cues). Certainly, the sheep showed no significant disadvantage in terms of speed of learning and response times for discriminating between human as opposed to sheep faces, which might argue in favour of this conclusion. However, against this is the fact that there was a significant improvement in learning speed and response times with familiar human faces in the same way as with sheep faces. This suggests that the task of discriminating between human faces was not in fact so easy since otherwise one would not have expected to see such marked improvement with familiarity.

As such, our findings would appear to be contrary to the studies in humans, which have shown that frequent visual contact is sufficient for the development of strong effects of inversion with faces of non-human species (Diamond and Carey, 1986) or handwriting (Bruyer and Crispeels, 1992) and to activate certain areas of cortex such as the Fusiform Face Area (Gauthier et al., 1999). They are also contrary to the findings that monkeys show an inversion effect to human faces but not their own species (e.g. Wright and Roberts, 1996), a result which would imply that the effect of configural coding may be used especially for the discrimination of human face stimuli.

It seems therefore that for sheep there is perhaps some innate predisposition to be able to identify sheep faces using specialised neural mechanisms that can encode configural cues. Other visual objects, including faces of other species, might not gain access to these same specialised systems even after a great deal of experience and training. It should be noted that in the human literature, Diamond and Carey’s expert subjects had several decades of experience with the stimulus family (dogs), which amounts to considerably more prior experience than the sheep in this study. On the other hand, Gauthier’s (Gauthier et al., 1999)
subjects had only 7 h training with the specially constructed ‘greeble’ stimuli, which was sufficient to result in right hemisphere face-sensitive areas being activated and to result in configurational coding effects (Gauthier and Tarr, 1997). Whilst we cannot be certain that sheep could never become experts recognising another species, it appears in this study that despite several years of natural experience with humans and a great deal of training in human face discrimination these animals have been unable to do so as yet.

To summarise, the experiment shows that while sheep are capable of learning to discriminate effectively between individual human faces at a level of performance that is similar to that of discriminating between sheep faces they do not appear to use the same specialised neural systems for configural encoding used for sheep faces. Instead, they appear to use unsophisticated feature detection methods similar to those used for other classes of visual object. Whilst it is presumed that experience with a type of visual stimulus is necessary to becoming expert in its recognition, this paper found that experience is probably not always sufficient. Ultimately, ‘nurture’ may be unable to overcome the effects of ‘nature’ in some forms of perception.

Acknowledgements

This work was supported by a BBSRC project grant.

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