

Functional asymmetry in sheep temporal cortex

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Sheep, like humans, show a bias in favour of the left visual field when discriminating familiar faces. This, in humans, is thought to be caused by a right hemisphere dominance for processing faces involving the temporal cortex. We have directly investigated inter-hemispheric differences in face-processing in sheep by recording the frequencies and response profiles of single cells in the temporal cortex which respond selectively to faces. While there was no evidence for increased frequencies of face-sensitive neurons within the right temporal cortex, or their relative selectivity for individual faces, there was a pronounced response latency difference between the two hemispheres. The cells in the left

hemisphere responding selectively to particular faces did so up to 400 ms later than those in the right and with a greater degree of temporal variability between cells. No hemispheric latency differences were found, however, in other cells responding to general visual stimuli or to many faces. The data suggest that, while specialised face-sensitive neural circuits in the right hemisphere may play a key role in the rapid (< 200 ms) identification and discrimination of facial identity, those on the left may be involved more with slower processes associated with integrating the emotional or mnemonic consequences of recognition. *NeuroReport* 13:2395–2399 © 2002 Lippincott Williams & Wilkins.

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INTRODUCTION

One of the most robust findings of face recognition studies in humans has been that of hemifield bias. It was originally noted by Wolff [1] that the left side of a face looks more like the owner than the right, when subjects looked in free viewing conditions at stimuli where one side had been mirrored onto the other. Subsequent studies have shown that faces presented wholly in one visual hemifield are recognised faster [2,3] and more accurately [4,5] on the left. Also when chimeric faces (where the left half of one face is combined with the right half of another) are presented [6–9], the left hemifield is more influential in the subjects' perceptions of faces. These effects are all thought to be caused by the greater use of the right hemisphere (RH) temporal cortex for face perception tasks [10,11].

Sheep are able to recognise [12] and remember [13] both sheep and human faces. Like humans they can recognise familiar faces using internal configural cues [14] and show impaired recognition of inverted faces but not other objects [12]. They also show a robust hemifield bias when perceiving faces [14], recognising faces more accurately from the left than the right side. Furthermore, studies using expression of the immediate early gene *c-fos* as a marker for neural activation have found the right temporal cortex to be more strongly activated during a discrimination task between pairs of faces than the left [15]. Sheep may, therefore, be a useful model with which to study the precise

nature of differential encoding of faces by neural circuits in the right and left temporal cortices using single-cell electrophysiological techniques.

Several candidate (non-mutually exclusive) mechanisms may give rise to perceptual asymmetry in face recognition. More cells in one hemisphere could be sensitive to faces, leading to greater processing of the contralateral visual hemifield. Alternatively, the hemispheres may respond with different latencies. Third, the cells in each hemisphere might respond to different characteristics of the faces (e.g. the configuration of features *vs* the qualities of each feature), such that one hemisphere is more or less specialised in its recognition of faces.

The current study aimed to distinguish between these hypotheses by comparing the sensitivity, selectivity and latency of face-sensitive cells in the left and right temporal cortices.

MATERIALS AND METHODS

Subjects: Two Horned Dorset ewes were used for RH unilateral electrophysiology. A further four sheep were implanted with bilateral recording wells. There was no evidence, from response times or proportions of cell types, that the RH recordings in the unilaterally and bilaterally recorded animals differed (nor was there any reason to

expect that they would) so the data from all six animals were pooled.

Procedure: We used standard methods for electrophysiological recording in the sheep [16,17]. Stainless steel recording chambers were implanted bilaterally or unilaterally over temporal cortex, under halothane anaesthesia. Starting 2 weeks after surgery animals were recorded from roughly once per week. For this they were restrained in a sling and the head was immobilised by the use of surgically implanted horn-bolts. The dura was anaesthetised using tetracaine and glass-insulated tungsten microelectrodes were introduced into the brain through guide-tubes using a hydraulic microdrive. Animals quickly became accustomed to the recording apparatus, and to being restrained in a sling during the recording sessions. Cardiovascular rates after the first session or two were normal, and the animals would ruminate, which they do only when calm. After the final recording session animals were given an anaesthetic overdose and several electrolytic lesions were made so that track locations could be reconstructed using standard histological techniques. The anatomical locations of the recordings are portrayed in Fig. 1.

Stimuli: All visual stimuli were presented by a computer connected to an LCD projector (Boxlight 3600AE, Boxlight Corp., USA) onto a back-projection screen 1 m in front of the animal. The projected images occupied roughly $65 \times 50^\circ$ of visual angle. All stimuli were in the PAL video format (25 frames/s at an interlaced resolution of 768×576 pixels). Images were arranged into several groups of 14 stimuli,

each of roughly 4 s in length and each repeated three times in a pseudo-random order. The stimuli within each set were separated by a fixation image lasting 5 s. Both moving video images and stills were used.

Initially, cells were screened using a variety of general stimuli (including faces, moving bars, natural scenes and non-face objects). Having identified a cell as being responsive to face-type stimuli, further sets of faces were shown to elucidate the degree of selectivity of the cell. These face sets included a variety of views (front, profile, inverted) of a number of different sheep (up to 12 different individuals) and humans (up to three different individuals) presented in a random sequence. A small range of auditory and somatosensory stimuli were also presented informally and used to exclude cells sensitive to general arousal. Eye movements were not formally recorded but the animals were positioned in such close proximity to the projection screen that with their limited capacity for eye movements the pictures shown must always have been in view.

Analysis and classification of cells: For cells showing reasonable levels of spontaneous activity their response to each stimulus was calculated as the percentage increase/decrease in firing frequency from a mean basal rate taken during the 2 s immediately preceding stimulus onset. For cells showing low or no activity preceding stimulus onset simple firing rate was used. From these responses cells were classified according to their sensitivity and selectivity to the various stimuli within groups. Responses of all cells were calculated from between three and nine repetitions of each stimulus.

The broadest classifications were simple visual and simple motion which meant that the cell's firing rate was significantly (*t*-test, $p < 0.001$) raised or lowered to several face and non-face visual stimuli, often including simple moving bars, compared with general auditory or somatosensory stimuli. Then, in order of increasing specificity, came the categories of face cell (responding more to faces than other stimuli, *t*-test $p < 0.01$), semi-specific face cell (responding to a class of faces such as sheep more than to other faces, *t*-test $p < 0.05$) and highly specific face cell (responding more to a single face than any other presented, *t*-test $p < 0.05$). At each increased level of categorisation the tests are performed on fewer cells, reducing the risk of family-wise error. This is why, for instance, the criterion is less for categorisation of a semi-specific face cell than for a visual cell given that the unit has already passed the more stringent statistical criterion of being a visual cell.

Peristimulus-time histograms (PSTHs) of the cell's response were averaged over all repetitions of the stimulus (or multiple stimuli if the unit was weakly selective). From these the cell's latency was calculated as the first bin for which the response was 2 s.d. higher than the basal firing rate. In addition the rise time was calculated as the time from the first significant response to the peak response. An example of cell classification and latency data is given in Fig. 2.

RESULTS

Sensitivity of cells to faces: From a total of 700 cells recorded from in the right temporal cortex, 168 (24.0%)

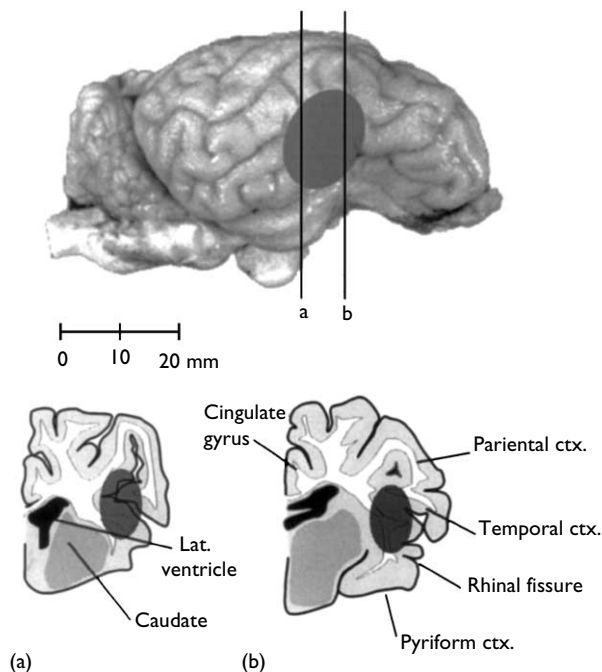


Fig. 1. Location of recording sites in this study. Upper: lateral view of sheep brain. The shaded region indicates where penetrations were made. Lower: schematic coronal sections of the right hemisphere showing the medio-lateral locus of cells recorded. The anatomical distribution of recordings was very similar in the two hemispheres.

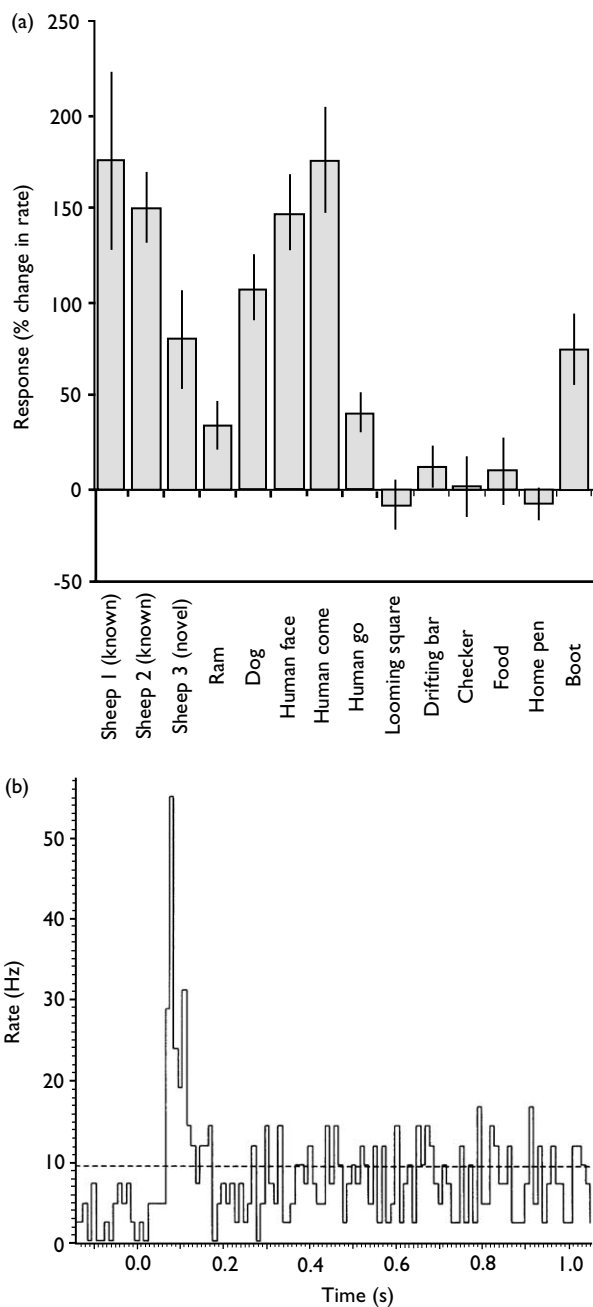


Fig. 2. Example responses of a right hemisphere cell (NI74 I2I) to 14 stimuli (12 repeats). (a) This cell responded to faces more than other stimuli ($t = 6.30$, $df = 166$, $p < 0.001$) and to familiar faces (including this human) more than unfamiliar ones. Thus it is characterised as a semi-selective face cell. (b) PSTH of the cells responses (10 ms bins) show that the first response significantly above baseline came after 85 ms with a further 10 ms rise-time before the peak response was reached.

showed visual responses. Of these visual cells, 67 (39.9%) were especially sensitive to faces, 11 (6.5%) to general visual motion and 90 (53.6%) could not be characterized other than to say they were visual.

In the left temporal cortex, 230 cells were recorded. In general, they showed a very similar distribution of response to cells in the right with 66 (28.7%) responding to one or

more visual stimuli. Of these, 34 cells (51.5%) were sensitive to faces, 6 (9.1% of the visual cells) to visual motion and 26 (39.4%) could simply be characterised as visual.

Selectivity of face cells: In the right temporal cortex, of the 67 face cells recorded, 14 (20.9%) responded to the sight of faces generally (non-specific face cells), 38 (56.7%) responded to a specific subgroup of faces such as sheep, familiar sheep, humans etc. (semi-specific face cells) and 15 (22.4% of face units, 2.1% of total) responded highly specifically to only a single sheep or human face from our set of face stimuli.

Of the 34 face-sensitive cells in the left hemisphere, four (11.8%) were activated generally by faces, 20 (58.8%) were semi-specific and 10 (29.4%) were highly specific. Relative numbers of the different visual units are shown in Fig 3.

Response latencies: Response latencies are shown for both hemispheres and all classes of visual cells (Fig. 4a). Unbalanced ANOVA was used to provide statistical analysis of the differences between the populations. This showed that there was a main effect of hemisphere ($F(1,176) = 10.09$, $p < 0.01$) with the cells on the left responding slower than those on the right. There was also a main effect of cell class ($F(4,176) = 5.09$, $p < 0.001$) indicating that more selective face cells respond slower than less selective ones, consistent with previous findings [18]. There was also a trend towards an interaction ($F(4,176) = 2.18$, $p = 0.073$), due to the fact that no hemisphere-dependent latency difference was observed for cells sensitive to general visual stimuli.

There was also more variability in response latencies across the population of LH than RH cells. Again this was

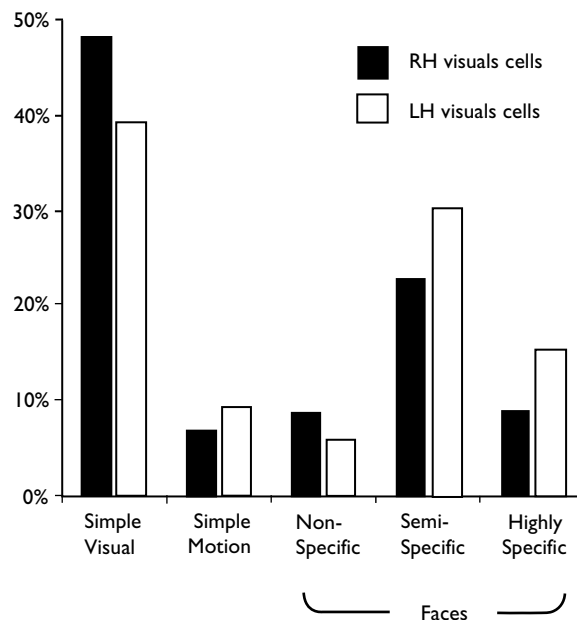


Fig. 3. Proportions of the major categories of cells as a percentage of the visually sensitive units in the right (RH; $n = 168$) and left (LH; $n = 66$) hemispheres. The differences in specificity between the hemispheres are well within the normal bounds of variation observed between animals.

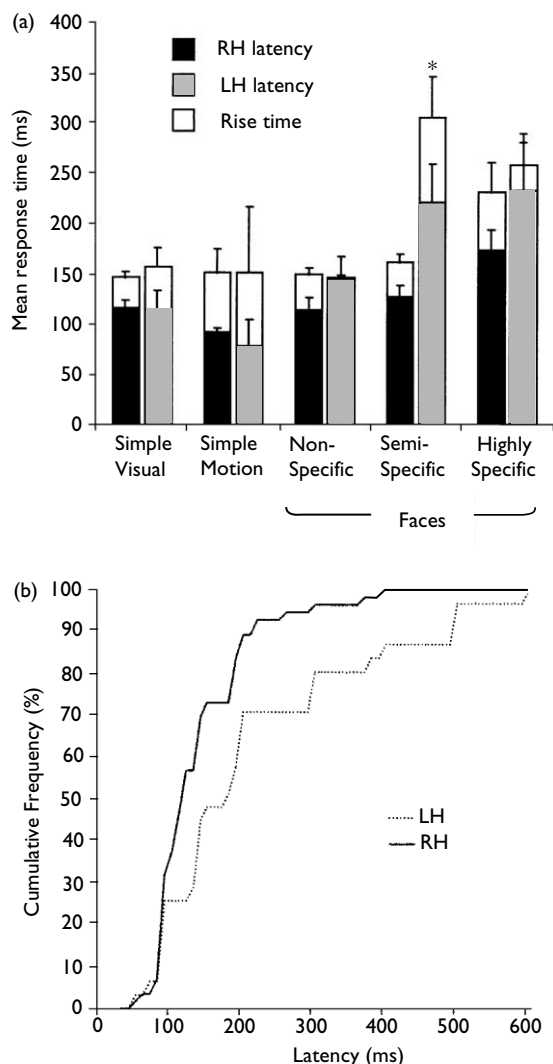


Fig. 4. Comparison of left (LH) and right (RH) hemisphere single cell response latencies and rise times. (a) mean latency and rise-time (time between latency and peak) for each type of unit. Bars show s.e. $*p < 0.05$ (t-test between hemispheres). (b) comparison of cumulative frequencies of face cells latencies (non-specific, semi-specific and highly specific). LH and RH are similar in proportions of cells up to 100 ms latency but the left then has a higher proportion of cells with longer latencies.

the case for semi-specific face cells (s.d between RH units = 67.6 ms, LH = 153.5 ms) and for highly specific units (s.d for RH = 86.4 ms, LH = 174.8 ms) but was not the case for cells responding to faces in general (s.d for RH = 49.3 ms, LH = 45.58 ms).

To verify that the differences in response times were not an artefact of response magnitude (a strongly responsive unit might rise more quickly above a statistical threshold), correlation coefficients were calculated throughout the data. None of these yielded a significant correlation between response magnitude and latency (non-specific face cells, $r = -0.12$, $df = 14$; semi-specific face cells, $r = 0.02$, $df = 52$; highly specific cells, $r = 0.03$, $df = 18$; all face cells combined, $r = 0.06$, $df = 89$). Thus response magnitude appears to

explain very little of the variance in response latency observed here.

DISCUSSION

This study has shown that under passive viewing conditions cells in the temporal cortex of the left hemisphere of sheep that selectively encode faces are found as frequently as cells in the right hemisphere. Furthermore cells in the two hemispheres showed very similar levels of encoding specificity across the different face stimuli used. However, face-sensitive cells selective for category of face or a specific familiar individual respond up to 400 ms slower in the left hemisphere than in the right. For cells responding more generally to visual stimulation, or to any face, there was no difference in the response latencies of the two hemispheres.

The differences in response latencies in left and right temporal cortices are consistent with findings published by Seck *et al.* [19] on human epileptic patients. They found that visually evoked potentials specific to familiar faces occurred in both hemispheres, with a very fast component between 50 and 90 ms occurred predominantly in the right hemisphere but later field potentials (190–600 ms) were observed bilaterally.

It is unclear why there would be such a large delay before the response of the left hemisphere neurons. Both humans [20] and sheep (Kendrick and Peirce, unpublished observations) are capable of identifying faces in ≤ 600 ms. The psychophysics tasks used necessarily include time to plan and execute the motor responses, which would require at least 200 ms. Therefore it seems likely that the cells responding in the range 400–600 ms are not contributing critically to the discrimination of faces, given that the perceptual task can be completed before these cells respond. They would also appear to be redundant in such tasks given that other cells with similar sensitivities respond several hundred milliseconds earlier. It appears most likely therefore, that these cells are involved in later processing consequent on recognition, such as integration with previous experience or perhaps the emotional sequelae of recognising familiar individuals.

Our failure to find evidence for higher numbers of, or more selective encoding of faces by, face-sensitive cells in the right temporal cortex is perhaps surprising given our strong behavioural and neuroanatomical evidence for right hemisphere dominance in sheep face recognition [14,15]. However, the right hemisphere dominance in those studies was revealed in tasks of active discrimination between faces, quite different from the passive perception of faces used in this experiment. It is entirely possible that the active discrimination tasks give rise in some way to greater hemisphere bias. However, whether or not there is a task-dependent difference in the number of face-sensitive cells, our data make it clear that nature of face-selective neural circuits in the left and right temporal cortices may be very different.

The fact that the latency difference was only observed for the more specific cells (sensitive to certain individuals or groups of individuals) is interesting since it indicates that the two hemispheres have similar capabilities in terms of identifying the simple presence of a face. When required to

determine further details such as the species or identity of that face however, the right hemisphere has a very pronounced speed advantage. Furthermore, the more selective face cells in the right hemisphere all respond with a similar latency, whereas within the left hemisphere the response times are more variable between units. The more consistent activation latency of several neurons may also result in an advantage of mass action for the right over the left hemisphere. Again, however, this is not the case for less selective neurons, which showed little ensemble variability in either hemisphere. Therefore it appears that the responses in the two hemispheres only differ at the level where advanced classifications are being made, such as discrimination between faces rather than discrimination between face/non-face. This is very much consistent with the large literature suggesting that discrimination between faces requires recognition of subtle configural differences (a process thought to be conducted predominantly in the right hemisphere), whereas discriminating between a face and a non-face requires no such complex processing.

In summary, we have produced the first clear evidence at the single cell level that the neural circuits encoding for facial identity leading to recognition in sheep may be predominantly localised in the right hemisphere. The left hemisphere shows a similar but very much delayed response. This may reflect a functional involvement of the left hemisphere in mediating post-recognition integrative

responses in relation to memory or emotional significance that could either be independent of, or dependent upon, the process of facial identification occurring on the right.

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