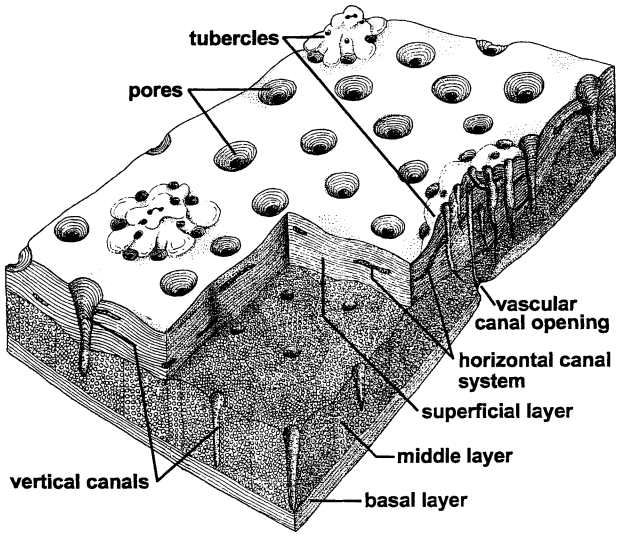

FIG. 4 Late Cambrian vertebrate from Australia. Block diagram summarizing the three-layered structure of the dermal armour with its pore canal and vascular systems.

tion of histological characters, in a sheet-like phosphatic skeleton which lacks odontode units, thereby contradicting the odontode model, but conforming to an alternative view that enamel-like tissues may have been most primitive for vertebrates[23]. The highly mineralized surface layer may also have served as a store for calcium and phosphate processed through the epithelium[24]. Another idea relates the origin of the dermal skeleton to a dentine sensory system, with mineralized sheets fixing their position in the tissue[25]. The well-developed pore-canal system in our new material suggests an alternative sensory function, perhaps neuromasts as part of a rudimentary lateral line system. The polygonal structure of the middle layer is reminiscent of the tissue cosmine in Devonian sarcopterygian fishes[26], in which the flask chambers have been interpreted as sites for electroreceptors[27]. The pore canals terminating within the middle layer (Fig. 4) could have had a similar function, differing mainly in the more rudimentary system of connection through the horizontal canals. The discovery of a pore-canal system in various agnathan and gnathostome groups suggests that it formed an essential part of the primitive laterosensory system of vertebrates[1,28]. In contrast, the fragments of *Anatolepis* lack structures interpretable as parts of a laterosensory system, the 'pore canals' recently described[6] as traversing the laminar tissue between the odontodes being quite different in size and structure, with no evidence of interlinking by horizontal canals. This laminar tissue in *Anatolepis* has been compared with 'hyaloine' in some recent teleost scales, but this is a mesodermally derived tissue formed by osteoblast-like cells, in which the only spaces are for attachment fibre bundles.

The discovery in the Late Cambrian of two completely different types of phosphatic dermal armour suggests experimentation in initial evolution of the vertebrate skeleton, which must have occurred much earlier than previously assumed. This is consistent with the prediction that major chordate clades (tunicates, craniates) had already evolved in the main burst of the Cambrian explosion[29]. This new material combines a pore-canal system with enamel-like hard tissues, implying that these may have preceded the formation of bone and dentine, with both euconodonts[3,12,13,22] and *Anatolepis*[6,14] representing divergent specializations within the early diversification of vertebrate hard tissues. □

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A differential neural response in the human amygdala to fearful and happy facial expressions

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THE amygdala is thought to play a crucial role in emotional and social behaviour[1]. Animal studies implicate the amygdala in both fear conditioning[2] and face perception[3]. In humans, lesions of the amygdala can lead to selective deficits in the recognition of fearful facial expressions[4,5] and impaired fear conditioning[6,7], and direct electrical stimulation evokes fearful emotional responses[8]. Here we report direct *in vivo* evidence of a differential neural response in the human amygdala to facial expressions of fear and happiness. Positron-emission tomography (PET) measures of neural activity were acquired while subjects viewed photographs of fearful or happy faces, varying systematically in emotional intensity. The neuronal response in the left amygdala was significantly greater to fearful as opposed to happy expressions. Furthermore, this response showed a significant interaction with the intensity of emotion (increasing with increasing fearfulness, decreasing with increasing happiness). The findings provide direct evidence that the human amygdala is engaged in processing the emotional salience of faces, with a specificity of response to fearful facial expressions.

Facial expressions are a mechanism through which internal emotional states and intentions become available as external signals, consequently the face is vital in social cognition[1,9,10]. The primate amygdala is thought to be involved in processing facial expression and in controlling emotional and social behaviour[1,2]. Direct evidence for its role in humans is limited to neuropsychological studies of subjects with rare selective amygdala lesions[4,5], and electrophysiological studies of epileptic patients[8]. Using normal volunteer subjects, we tested whether the human amygdala is critical in processing fearful expressions, as suggested by the lesion studies[4,5]. We measured regional cerebral blood flow (rCBF) in five subjects while they viewed grey-scale images of emotionally expressive faces taken from a standard set of pictures of facial affect[11]. The faces depicted either happy or fearful expressions, and for each emotional category and individual face a range of six levels of intensity was produced by computer graphical manipulation[12] (Fig. 1). For each subject, separate scans were acquired for each intensity level in a 2×6 (category $\times$ intensity) factorial experimental design. For each presented face, subjects were simply required to make a gender classification (male or female) by pressing left or right response buttons. No explicit recognition or categorization of emotional expression was required during the scans, and post-scan debriefing confirmed that subjects were not aware that the implicit emotional variable was crucial in the experimental design.

The rCBF pattern produced by the presentation of fearful faces (contrasted with happy) showed the left amygdala and left periamygdaloid cortex as the most significant areas of activation ($P < 0.05$, corrected). There was no activation of the right amygdala, even at low thresholds. The statistical parametric map (SPM) of this contrast and the associated mean adjusted rCBF values for the happy and fearful conditions at the maximal point of activation are shown in Fig. 2. Other areas, that would have been judged significant if they had been predicted beforehand, included the left cerebellum, left cingulate gyrus and right superior frontal gyrus ($P < 0.001$, uncorrected). A contrast of happy with fearful expressions, on the other hand, was associated with activations in the right medial temporal gyrus, right putamen, left superior parietal lobe, and left calcarine sulcus ($P < 0.001$, uncorrected). The coordinates and Z scores for these activations are given in Table 1.

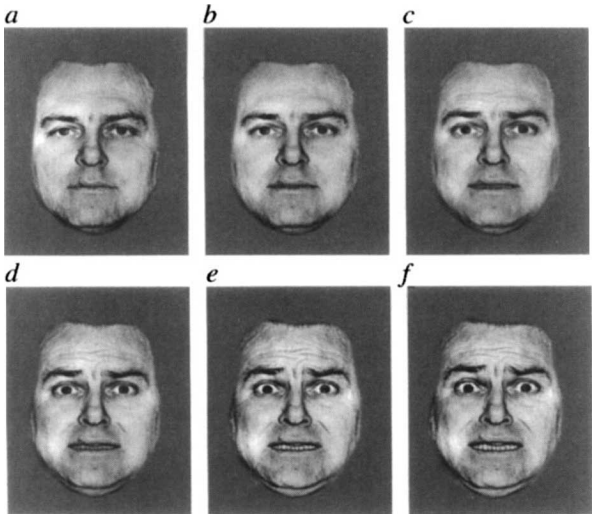

FIG. 1 Faces *a* and *e* are prototypical neutral and fearful expressions. Faces *b*–*d* are interpolated between these prototypes, using computer morphing procedures[12] to shift the shape and pigmentation of the neutral prototype towards the fear prototype; *b* involves 25% fear (and 75% neutral), *c* 50% fear (and 50% neutral), *d* 75% fear (and 25% neutral). Face *f* is an enhanced 125% fear expression, created by shifting the shape of the fear prototype 25% away from neutral (increasing by 25% any differences from neutral).

TABLE 1 Regions of activity in response to emotional expression contrasts

Area	Coordinates (*x*, *y*, *z*)	*Z* score
Fearful–happy		
Left periamygdaloid cortex (BA34)	−14, −8, −20	4.26
Left amygdala	−18, −6, −16	3.86
Left cerebellum	−42, −68, −20	3.57
Right superior frontal gyrus (BA6)	22, 4, 64	3.22
Left cingulate gyrus (BA23)	−10, 28, 16	3.18
Happy–fearful		
Right medial temporal gyrus (BA21)	54, 4, −20	3.55
Right putamen	22, −4, 12	3.48
Left superior parietal lobule (BA5)	−28, −40, 60	3.41
Left superior parietal lobule (BA7)	−24, −72, 44	3.12
Left calcarine sulcus (BA17)	−10, −92, 4	3.06

Regions selectively activated when the different emotional conditions are contrasted. The contrasts were fearful relative to happy expressions (top) and happy relative to fearful expressions (bottom). Coordinates of the maximal point of activation, Brodmann areas (BA), and the associated Z values are shown. The activations in all regions are significant at $P < 0.001$ (uncorrected). In the amygdala, the only area predicted to show a response, this is equivalent to a significance level of $P < 0.05$, corrected for multiple spatial comparisons in a $2 \times 2 \times 2$ cm search region[30]. The activations in the other brain regions would have had the same corrected level of significance if they had also been predicted beforehand. All P values are one-tailed.

The interaction between the neural responses to emotional category and emotional intensity was examined by applying orthogonal contrasts. Thus, the voxels that showed a significant response in the contrast of fearful versus happy faces (as in Fig. 2) were subjected to a second orthogonal contrast to determine the presence of a differential response to varying emotional intensity (increasing activation with increasing fearfulness and decreasing activation with increasing happiness). The left amygdala was the only significant area in this interaction (Fig. 3). The rCBF response in the left amygdala to changes in the intensity of facial expression shows monotonic increases in left amygdala activation from the most happy condition to the most fearful (Fig. 3).

Our results provide direct evidence that the human amygdala is involved in a neural response to fearful facial expressions. The nature of our experimental design, in which faces were classified by gender and not by expression, suggests that amygdala activation is not contingent upon explicit processing of facial expression, a finding in-keeping with electrophysiological data[13]. The differential response within the amygdala, to fearful as opposed to happy faces, complements psychological data based on multidimensional scaling, indicating that these facial emotions are at opposite ends of a spectrum of similarity[4]. The unilateral response in the left amygdala parallels findings in a study of procaine-induced emotional states[14] where left (but not right) amygdala rCBF correlated positively with fear and negatively with euphoria. It is also consistent with a study of patients with unilateral amygdala damage which found that ratings of emotional intensity in facial expressions were significantly lower with left amygdala lesions compared with right[15]. Bilateral amygdala lesions may not always be sufficient to impair recognition of fearful expressions[16], indicating that other neural systems can perform this role. The additional activations associated with fearful faces, in the cerebellum, frontal lobe and cingulate gyrus, which were not predicted, may indicate brain areas, outside the amygdala, which are involved in responding to fearful expressions.

Neurophysiological studies[3] in the macaque and neuroimaging experiments[17,18] in humans suggest neural segregation of the processing of facial identity and facial emotion. The human studies used explicit tests of emotional recognition and discrimination in which the emotional category and intensity of facial expression were not variables of interest. In our experiment the emotional variable was implicit, and the parametric factorial design provided a means to determine a differential response to both emotional category and intensity. These differences in experimental design may explain why our study of facial emotion did not observe activation in the areas of prefrontal and cingulate cortices reported in the earlier PET experiments. It is possible that there was a common response in these areas in the fearful and happy conditions resulting in no net activation when these emotions are contrasted directly. Alternatively, these frontal areas may be involved in the explicit rather than implicit processing of facial expression, and therefore have a primary role in attentionally related processes.

The primate amygdala receives substantial inputs from temporal visual-association[19–21], and contains neurons that respond selectively to individual faces[5,22,23]. The amygdala also has a strong anatomical link with the autonomic nervous system[24]. This connectivity, coupled with the selectivity of its response, suggests that the amygdala is appropriately placed in relation to sensory and autonomic systems to enable integrated responses to the emotional significance of complex stimuli. Integrated responses to threat or danger, without the necessity of higher level processing, can be mediated by the amygdala[1,2]. There is evidence in humans that amygdala damage impairs the formation of conditioned autonomic responses to aversive stimuli[8,9]. We suggest that perceiving an expression of fear in a conspecific may trigger an automatic response to potential danger that accounts for the observed amygdala activation in response to fearful faces.

Ethnological studies suggest that facial expressions of emotion are innate, automatic, and of critical importance in social behaviour[9,10]. In the nonhuman primates there is evidence that the amygdala is an important component of the neural system involved in social behaviour. Monkeys that have had their amygdala ablated are tame[25,26], and no longer make appropriate responses to signals of danger or threat[1]. Radiotelemetry recordings of amygdala activity in monkeys during social interactions show the highest responses to ambiguous or threatening situations (for example, threat face display), and the lowest to tension-lowering behaviours (such as grooming and huddling)[27]. Our observation of a differential response in the left human

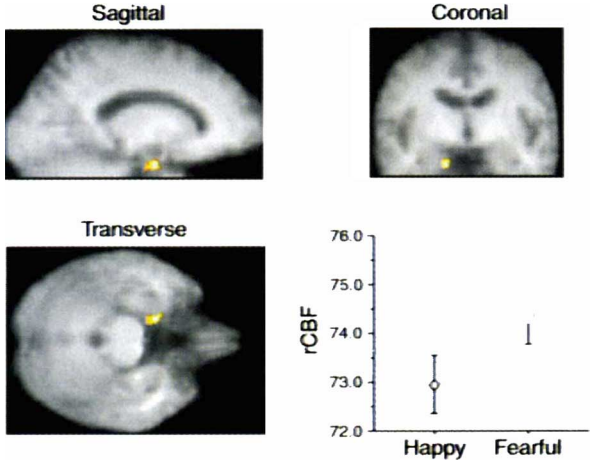

FIG. 2 A statistical parametric map (SPM) showing activation of the left amygdala, together with a graphical display of the mean adjusted rCBF values. An uncorrected P value of 0.01 was used as the threshold for the contrast of the fearful with the happy conditions. Views of the brain are shown for orthogonal slices at the pixel of maximal activation within the left amygdala ($x = -18$, $y = -6$, $z - 16$). The significant area of activation is displayed on the mean MRI image produced from the co-registered structural MRIs from all five subjects. In the graph, unweighted means (± 2 s.e.m.) of the rCBF values at the pixel $x = -18$, $y = -6$, $z = -16$ are shown for the five fearful and five happy conditions. The difference between the means is significant ($P = 0.0014$) on an unpaired t-test.

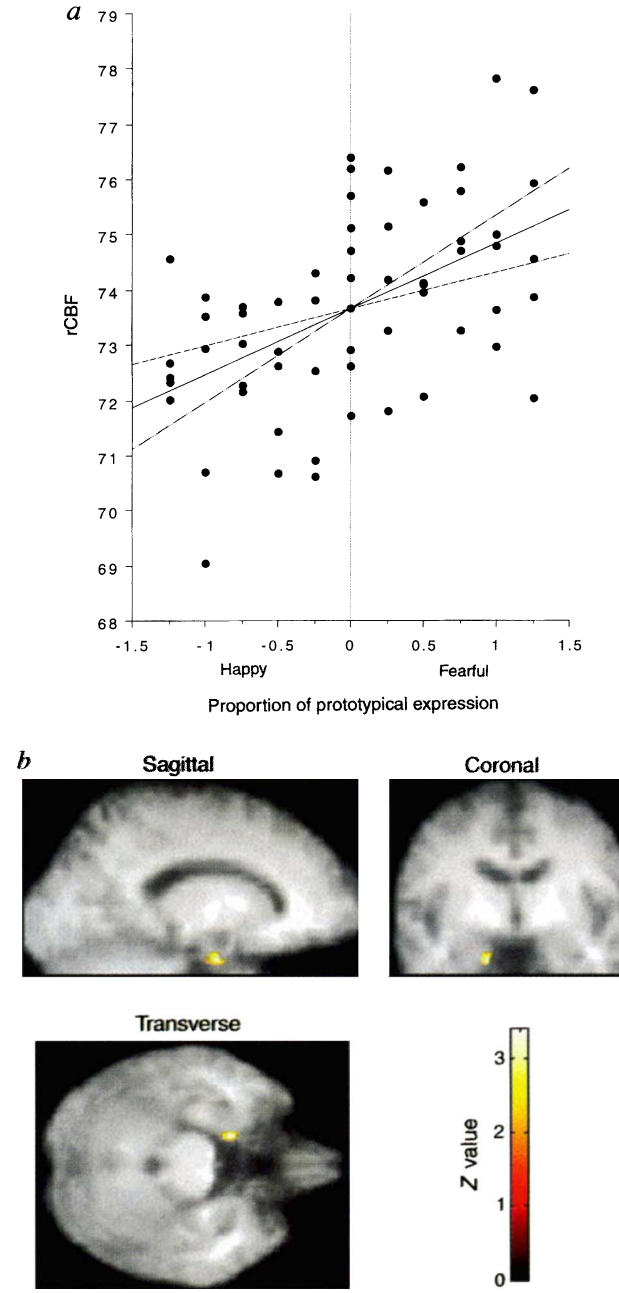

FIG. 3 a, rCBF values and b, statistical parametric maps (SPM) showing activation of the left amygdala in the interaction of emotional category and intensity. The SPM is the result of two orthogonal contrasts (see text). An uncorrected P value of 0.03 was used for both contrasts giving a resultant value of 0.0009 for the interaction. The views of the brain are the same as in Fig. 2. The graph plots the rCBF values in ml dl^{-1} min^{-1} for all conditions and all subjects at $x = -18$, $y = -6$, $z = -16$ (the pixel of maximal activation). The x axis represents the proportion of the prototypical expression in the face stimuli, with fearful being positive (100% = 1), and happy negative (100% = −1). A regression line has been fitted to the data (with broken lines representing 95% confidence intervals for the gradient of the slope. Correlation coefficient r, 0.514.

amygdala to faces that embody either fearful or happy expressions indicates that it may play a similar regulatory role in human social behaviour. □

Methods

Subjects. Four male subjects and one female subject (mean age 42.8 years) took part in the study (approved by the local hospital ethics committee and ARSAC(UK)). All subjects were healthy, with no past history of psychiatric or neurological illness, and were not on any medication. A sixth post-menopausal female subject (age 62 years) was scanned but she was later found to be receiving hormone replacement therapy and was therefore excluded. Inclusion of the data from this subject in the analysis still produced significant activation of the left amygdala ($Z = 3.35$).

PET scan acquisition and analysis. Scans of the distribution of $H_2{}^{15}O$ were obtained using a Siemens–CPS ECAT EXACT HR$^+$ PET Scanner operated in high sensitivity three-dimensional mode. Subjects received a total of 350 MBq of $H_2{}^{15}O$ over 20 s through a forearm cannula. Images were reconstructed into 63 planes, using a Hann filter, resulting in a 6.4 mm transaxial and 5.7 mm axial resolution (full-width at half-maximum). The data were analysed with statistical parametric mapping (SPM 95 software, Wellcome Department of Cognitive Neurology, London) implemented in Matlab (Mathworks, Sherborn, MA). After initial realignment, mean PET images from each subject were scalp-edited and used as a template to edit all 12 individual PET images. Structural magnetic-resonance images (MRIs) from each subject were co-registered into the same space. The scans were then transformed into a standard stereotactic space[28]. The scans were smoothed using a gaussian filter set at 12 mm full-width at half-maximum. The rCBF measurements were adjusted to a global mean of 50 ml dl^{-1} min^{-1}. A blocked (by subject) ANCOVA model was fitted to the data at each voxel, with a condition effect for each level of emotional intensity, and global CBF as a confounding covariate. Predetermined contrasts of the condition effects at each voxel were assessed using the usual *t*-statistic, giving a statistic image for each contrast. The method of SPM data analysis is described in detail in refs 28 and 29.

Experimental design. During each scan, 10 photographs of faces were presented, one at a time, on a computer monitor screen. Each presentation lasted for 3 s, followed by a 2-s interval in which the screen was blank. The 10 faces were of different individuals (5 males and 5 females), but all had the same category and intensity of emotional expression. The faces of the same 10 individuals were used in all 12 scans, in a randomized order. The emotional category and intensity of the faces were varied systematically across scans. The order of presentation of happy and fearful conditions was counterbalanced across subjects. The six different intensity levels were given in a counter-balanced order within and across subjects. In the gender-classification task during scanning, all five subjects identified correctly 90–100% of the time.

Behavioural tests. The validity of the different emotional categories and 'morphed' intensity levels was confirmed using rating and discrimination tests performed on the same subjects, after scanning. In classifying the category (fearful, happy, neutral or 'other'), 96.5% of responses were correct. Subjects then rated the intensity of expression of the face on a 7-point scale. These ratings correlated well with the proportion of the fearful or happy prototype in the morphed face (correlation coefficients: $r = 0.772$ for fearful, $r = 0.826$ for happy). In a separate discrimination test of emotional intensity, different faces were presented in pairs, and subjects selected the more intense expression. Again, there was a close agreement between perceived and 'morphed' intensities: 69.4% of ratings agreed for pairs differing by 25% in their percentage of prototype, 83.3% agreed for pairs differing by 50%, and there was 100% agreement for pairs differing by >50%.

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Precisely correlated firing in cells of the lateral geniculate nucleus

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SIMPLE cells within layer IV of the cat primary visual cortex are selective for lines of a specific orientation. It has been proposed that their receptive-field properties are established by the pattern of connections that they receive from the lateral geniculate nucleus (LGN) of the thalamus[1–5]. Thalamic inputs, however, represent only a small proportion of the synapses made onto simple cells[6–8], and others have argued that corticocortical connections are likely to be important in shaping simple-cell response properties[9–11]. Here we describe a mechanism that might be involved in selectively strengthening the effect of thalamic inputs. We show that neighbouring geniculate neurons with overlapping receptive fields of the same type (*on*-centre or *off*-centre) often fire spikes that are synchronized to within 1 millisecond. Moreover, these neurons often project to a common cortical target neuron where synchronous spikes are more effective in evoking a postsynaptic response. We propose that precisely correlated firing within a group of geniculate neurons could serve to reinforce the thalamic input to cortical simple cells.

The projections from the retina to the thalamus are both divergent and convergent. Individual retinal ganglion cells diverge to connect to at least four different geniculate neurons[12]. Conversely, geniculate neurons often receive convergent input from two or more ganglion cells[13]. Although slow correlations have been noted between geniculate neurons[14–16], little attention has been paid to a faster synchrony that may be caused by common input from divergent retinal afferents. Here we have found that extremely fast correlations do exist, and propose a role for them in the transmission of information from thalamus to cortex.

In simultaneous recordings from pairs of closely positioned geniculate cells (electrodes 100–400 μm apart), we occasionally observed firing patterns that were tightly correlated at the 1-ms timescale. These fast correlations were narrower and often stronger than other correlations previously studied in the visual system: between retinal ganglion cells[17–19], between geniculate cells with non-overlapping receptive fields[15,16], between geniculate and cortical cells[3,4] or between cortical cells[20–22].

The strongest fast correlations were between geniculate cells with very similar receptive fields (same position, sign, size and timing). Figure 1*a* shows the receptive fields of two pairs of *on*-centre geniculate X cells calculated by reverse correlation[23,24]. For

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