

Face Cells: Separate Processing of Expression and Gaze in the Amygdala

A neuroimaging study in monkeys has shown that separate regions of the amygdala are responsive to facial expression and gaze/head orientation.

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A significant body of research has addressed the role of the amygdala in processing visually observed faces, particularly facial expressions. Functional neuroimaging and brain lesion studies in humans have focused on this structure's role in processing facial signals of fear [1,2], but the evidence points to a wider, but as yet poorly specified role in processing various facial cues including eye gaze [3,4]. As reported recently in *Current Biology*, Hoffman *et al.* [5] have demonstrated, using functional magnetic resonance imaging (fMRI) in monkeys, that facial expressions and gaze/head orientation engage distinct sections of the amygdala, with the basolateral complex (the lateral, basal and accessory basal nuclei) showing greater activation to threatening than appeasing facial expressions irrespective of gaze direction, and the lateral extended amygdala (the central nucleus and bed nucleus of the stria terminalis) showing an increased response to averted relative to direct gaze irrespective of emotional expression (Figure 1). This striking dissociation is rooted in a strong history of face perception research in non-human primates that has influenced models of human face perception for over 30 years.

Pioneering single-cell recording research by Gross and colleagues [6,7] in the 1970s and 1980s identified neurons in the inferotemporal cortex that respond preferentially to faces relative to other object categories. Numerous studies followed and it was soon apparent that the inferotemporal cortex and superior temporal polysensory area of the superior temporal sulcus contain cells tuned

to facial expressions, head orientations, gaze directions and even individual identities [8,9]. The existence of cells coding identity fuelled the popular but often ridiculed concept of 'grandmother' cells — the idea that there is a single neuron coding each person you know, particularly your granny — but this extreme reductionist approach was soon dismissed in favour of ensemble coding, with face representations distributed across a network of cells coding different facial dimensions [8].

Single-cell recording provided important insights into the neurophysiology of face perception but begged obvious questions that subsequent human functional imaging studies attempted to address — are the same neural regions involved in human face perception, and do humans show separable neural coding of the same facial characteristics? Over 30 years since Gross and colleagues [6,7] first identified 'face cells', cross-species comparisons between humans and monkeys are now being made using the same basic fMRI technology, providing an exciting new episode in the neuroscience of face perception.

The new fMRI study by Hoffman *et al.* [5] builds on earlier cell recording research investigating the neural coding of faces in the amygdala. Initial work showed that this structure contains cells responsive to faces [10], while more recent work by Gotthard *et al.* [11] demonstrated that facial identity and facial expression are coded by both separate and common neuronal populations in the basolateral amygdala [11]. Hoffman *et al.*'s [5] observations that the basolateral amygdala shows an increased change in the blood-oxygen-level-dependent

(BOLD) signal — detected by the fMRI technique — for threat relative to appeasement is mirrored by Gotthard *et al.*'s [11] finding that neurons responsive to threat expressions were more likely to show increased activation, whereas the majority of neurons coding appeasement expressions showed decreased activation.

The more significant finding made by Hoffman *et al.* [5] relates to the role of the lateral extended amygdala in processing gaze/head orientation, with averted gaze/heads producing significantly more activation than gaze/heads oriented towards the observer. This raises interesting questions. Cells in the superior temporal sulcus are sensitive to different gaze and head orientations [9,12]; however, there are no major projections from the superior temporal sulcus to the lateral extended amygdala. So presuming that the latter receives gaze information from the former, how does it get there?

One possibility is the information comes via the very limited projections from the superior temporal sulcus to the central nucleus (a component of lateral extended amygdala). Another is that it comes via the basolateral amygdala, which receives projections from anterior temporal regions implicated in face perception — the superior temporal sulcus and inferotemporal cortex (Figure 1).

In the case of the latter route, the basolateral cells sensitive to different head orientations may be intermixed and show a similar BOLD response — as in the superior temporal sulcus [9,12] — so any separable coding is undetected by standard fMRI contrasts. Given that the superior temporal sulcus activation in the study by Hoffman *et al.* [5] showed no difference between averted and directed heads/gaze, this is a distinct possibility that a single-cell recording investigation of gaze and head orientation processing in the amygdala could help address.

Another question that Hoffman *et al.* [5] address is in what sense does the lateral extended amygdala contribute to gaze processing? The authors propose

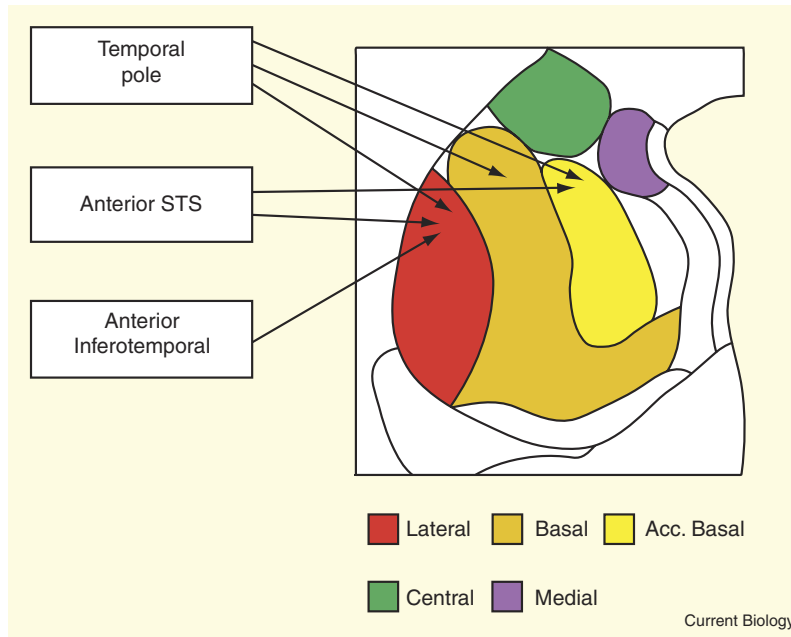


Figure 1. Pathways to the amygdala.

A summary of the major projections from the anterior inferotemporal cortex (TE), anterior superior temporal sulcus (STS), and temporal pole (TG) to the amygdala, as outlined by Amaral *et al.* [18]. The lateral, basal, and accessory basal nuclei constitute the basolateral amygdala, while the lateral extended amygdala comprises the central nucleus and bed nucleus of the stria terminalis (latter not shown).

that it may relate to the role of the central nucleus in attention, vigilance and orienting behaviour, and note its connections with subcortical structures involved in autonomic regulation. Consistent with this, they demonstrate that the monkeys showed increased autonomic arousal, in the form of increased galvanic skin response, to averted relative to directed heads/gaze, but no difference among emotional and neutral expressions. It is of interest that human research has identified increased amygdala activation, measured intracranially, and increased galvanic skin response, or 'orienting response', as two components of the 'orienting complex' that functions to "orient behaviour and cognition towards significant stimuli" [13].

Thus, increased lateral extended amygdala activation and galvanic skin response to averted heads/gaze observed by Hoffman *et al.* [5] may reflect the social and behavioural salience of these cues to monkeys. Hoffman *et al.* [5] are careful to point out that specific head orientations or expressions may have different 'behavioural

salience' for monkeys and humans. In fact, human functional imaging research to date has shown increased amygdala activation to direct rather than averted gaze, and it is eye contact that produces increased autonomic arousal in humans [14]. Nevertheless, despite these cross-species differences the important point that deserves further exploration is that the basic concept of the 'orienting complex' may be shared by both species and may have similar neural and physiological correlates. An interesting question for future work is how the arousal value of various facial cues modulates the fronto-parietal attentional networks that mediate appropriate orienting responses.

Hoffman *et al.*'s [5] study, together with other recent fMRI research in monkeys [15–17], adds to a continually developing literature investigating the neural basis of face perception. We look forward to the next exciting instalment.

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