Emotion 2: The neural bases of emotion

Aims and objectives

In this lecture, we summarise current ideas about the neural bases of emotion and the evidence that different brain areas may underlie different emotional states. Key learning objectives are that you will:

- Understand the role of the limbic system in general, and amygdala in particular, in emotion
- Appreciate how modern scanning techniques are advancing our understanding of emotion
- Understand the neural encoding of disgust responses
- Make links between the neural bases of emotion and previous aspects of the course

Recommended reading:

Toates, Carlson, Koob And Wishaw and all major textbooks in Psychobiology discuss these issues in varying detail and you are advised to look at several sources to get a broad view. There are also good concise review papers, such as:

Davidson & Irwin (1999) The functional neuroanatomy of emotion and affective style. *Trends in Cognitive Sciences,* 3: 11-21

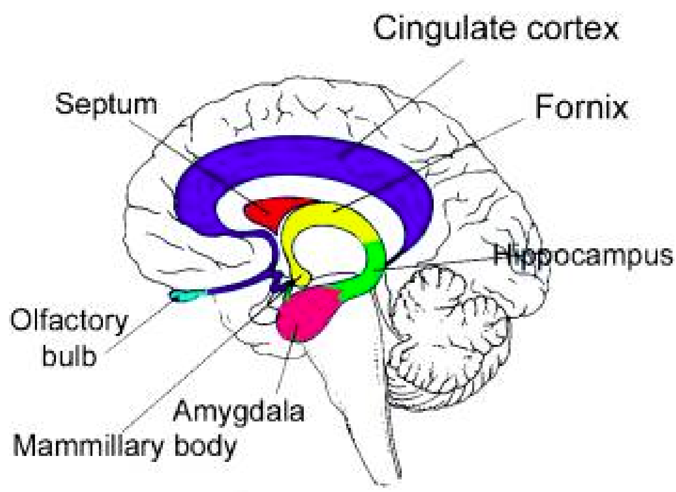
Holland, PC & Gallagher, M (1990). Amygdala circuitry in attentional and representational processes. *Trends in Cognitive Sciences, 3:* 65-73

A more comprehensive review was published recently:

Davidson, RJ, Jackson, DC & Kalin, NH (2000) Emotion, plasticity, context and regulation: perspectives from affective neuroscience. Psychological Bulletin, 126: 890-909.

Traditional neural views of emotion

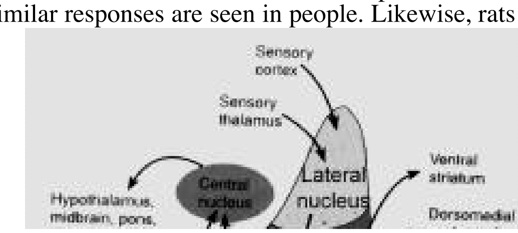
The view that the expression of emotion is controlled by the limbic system controls the expression of emotion was first introduced by Papez (1937).

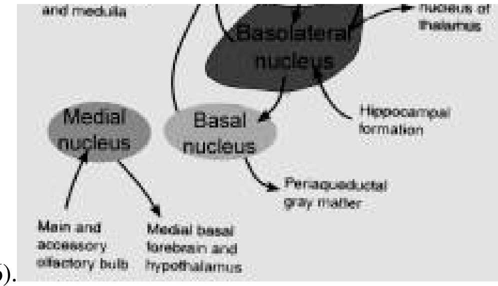


The limbic system consists of an inter-connected series of structures bordering the thalamus, & includes the amygdala, hippocampus, septum, fornix, olfactory bulb, mammillary body & cingulated cortex. Papez view was that the expression of emotion was due to actions of limbic structures on the hypothalamus, & the experience of emotion through projections to cortical sites.

The amygdala as emotional centre

Cells in the amygdala receive input from all sensory modalities, but many amygdaloid cells respond to complex stimuli only (e.g. faces) & some respond to all senses. The classic demonstration of the role of the amygdala in emotion is Kluver-Bucy syndrome, originally reported in monkeys whose amydalae had been removed (Kluver & Bucy, 1939). These animals showed: a) tameness & lack of fear b) indiscriminate eating patterns c) greatly increased & inappropriate sexual behaviour d) a tendency to attend & react to all visual stimuli e) oral examination of objects, all of which can be attributed to damage to the amygdala. Kluver-Bucy syndrome in humans is rare, but can be seen in some sufferers of encephalitic diseases. Electrical stimulation of the amygdala in animals produces fear and autonomic arousal, & similar responses are seen in people. Likewise, rats and





humans with lesions of the amygdala are less able to acquire the CER response (see lecture 16).

The amygdala has a complex structure, with five interconnected but functionally distinct areas. The lateral nucleus received sensory information which are relayed to the basolateral nucleus. This receives additional information from the hippocampus (associated with memory) and sends information to two other areas in the amygdala: the basal nucleus (which connects with the periaquaductal gray, associated with the freezing" response and pain control) and the central nucleus. Outputs from the latter include the lateral hypothalamus (sympathetic activation), parabrachial nucleus (increased respiration), ventral tegmentum (reward pathway & motivation), locus coeruleus (increased vigilance), trigeminal pathway (facial expression of fear) etc. Thus, the neuroanatomy alone suggest a central role in emotional processing of sensory information.

The amygdala as fear centre: some recent findings

- Recent neuropsychological data confirm and extend the view that the amygdala has a primary role in fearful responses.
  - Recognition of fear but not other emotions is impaired in patients with bilateral lesions of the Amygdala (Adolphs, 1995)
  - Prior conditioning of face-fear associations prime responding to angry faces both presented in masked and unmasked format (Morris et al., 1998 *Nature, 383*: 812-815)
  - Using FMRI, fearful, but not disgust, faces were found to cause activation of the amygdala (Breiter et al., 1996), even when the faces were presented at a subliminal level (Whalen et al., 1998)
  - Unpleasant, but not pleasant, stimuli activated the amygdala (Irwin et al., 1996).

Thus the amygdala has a wide range of roles relating to fearful responses.

The amygdala and acquired emotional responses

Since most fearful situations have to be learned, another important question is how this emotional learning is achieved. The clearest picture is seen for one particular behaviour: the startle response. A loud noise causes most species to show a classic startle response. This startle response can be enhanced if the noise is presented with a different cue which itself has been associated with a fear-evoking stimulus. Thus conditioned fear can augment the startle response. The underlying neural pathways can be summarised as:

The amygdala is not all negative?

Although no-one doubts the role of the amygdala in fear responses, some human studies suggest a broader role in emotional behaviour. Relevant recent evidence includes:

- Both positive and negative stimuli can activate the amygdala under certain conditions (e.g. erotic nude pictures, LaBar et al., 1998).
- Intensely pleasurable music activates the amygdala (Blood & Zatorre, 2001)
- Auditory perception of crying and laughing activates the right amygdala (Sander & Scheich, 2001)

Animal data provide even clearer evidence that the amygdala has a wider role than processing of information relating to fear. A full review of this role is beyond this lecture, but one particular element of amygdala function stands out: it has a specific role in attentional processes in relation to reinforcement. This fits well with one of the key functions of emotion: the focusing of attention on relevant stimuli. Attention in rats is measured by their orienting response (OR). If a novel stimulus is not followed by a reinforcer (such as food) the OR decreases with each exposure. If the light is now followed by food, the OR increases again in normal rats, but in those with lesions of the amygdala.

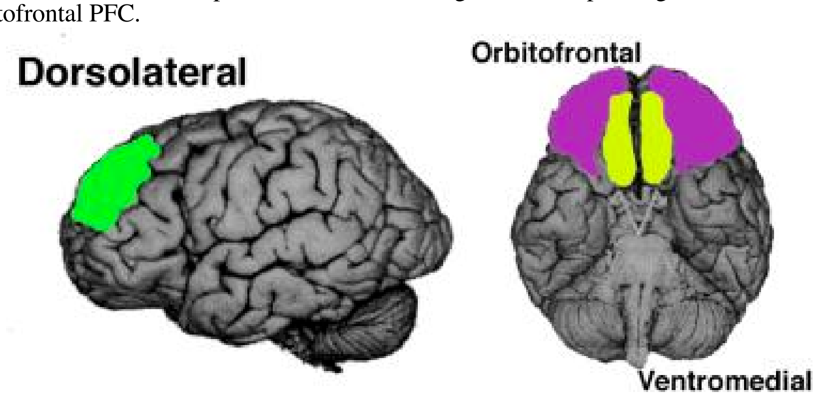
Not all emotions are in one place: the case of the disgusting insula.

Disgust responses are robust and are associated with an easily discernible facial expression. What stimuli evoke the disgust response is learned, mainly in early development. Recent research suggests that neural encoding of the disgust response involves different neural circuitry to other emotions, particularly fear, & does not involve the amygdala in particular. Key research findings to date include:

- Sufferers from Huntingdons Disease mis-identify facial expressions of disgust as fear
- People with obsessive-compulsive disorder also mis-recognise disgust
- These two disorders are both associated with disrupted functioning in the basal ganglia
- fMRI studies show different pattern of neural activation in response to disgust, fear and neutral facial expressions (e.g. Phillips et al., 1997: Nature *389*: 495-498)
- Whereas the amygdala is activated when viewing fearful faces, an area of the cortex known as the insula
- The insula is also involved in processing of taste stimuli.

The prefrontal cortex (PFC)

The experience of emotion appears to be centres in the prefrontal cortex. This again is a complex region, with three relevant areas: the dorsolateral PFC, ventromedial PFC and orbitofrontal PFC.



The most significant findings include:

a) Damage to the left PFC, but not equivalent areas of the right PFC, increases the likelihood of depressive symptoms
b) Positive emotional stimuli increase activity in the left PFC, whereas negative stimuli increases activation of the right PFC.
c) Lesions to the ventromedial PFC result in a general failure to anticipate future positive or negative consequences of actions (Bechara et al.)
d) Lesions to the orbitofrontal PFC reduces inhibition of behaviour & impairs the ability to translate judgements & conclusions about events into appropriate feelings & behaviours.

Summary

The neural encoding of emotions is complex, but although different emotions involve different brain areas, in each case the underlying structure fits with a model in which the significance of incoming sensory information is processed by mid-brain structures & those stimuli which have motivational significance (that is require action) lead to physiological changes associated with arousal, expressions of the relevant emotion & the experience of emotion (through cortical activation).

Martin Yeomans, October 2002