

*Entry for
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Emotion

Emotion is central to human life and intimately connected with *consciousness. Historically, the link with consciousness has led to a relative neglect of emotion as a subject of systematic scientific inquiry in comparison with other fields, such as *cognition. However, the last few decades have seen a significant increase in research on emotion, leading to important new discoveries of the brain mechanisms involved.

The concept of emotion can usefully be subdivided into two components: i) the *emotional state* that can be measured through physiological changes such as autonomic response, and ii) *feelings*, seen as the subjective experience of emotion. The latter is linked with *qualia and the hard problem of consciousness, that is to say, what is it *like* subjectively to experience an emotional state. How the brain gives rise to consciousness remains an unsolved problem, but it is becoming increasingly clear which brain areas are involved in producing and representing emotional states.

Ancient Greek and later Western philosophers have always discussed emotion, although the emphasis has almost exclusively been on its cognitive evaluation. Cognition and emotion have been regarded as separate areas, and subsequently, for the larger part of the 20th century, most scientific research focused on cognition at the expense of emotion. Notwithstanding, important theoretical advances were made by pioneering individuals such as Charles *Darwin (1872) who examined the evolution of emotional responses and *facial expressions. Emotions allow an organism to make adaptive responses to salient stimuli in the environment, thus enhancing its chances of survival.

In the 1880s William *James and Carl *Lange independently proposed the idea that rather than emotional experience being a response to a stimulus, it is the perception of the ensuing physiological bodily changes. The James-Lange theory suggests that we do not run from the bear because we are afraid but that we *become* afraid because we run.

William *Cannon (1929) offered a detailed critique of the James-Lange theory showing that surgical disruption of the peripheral nervous system in dogs did not eliminate emotional responses as would have been predicted by the theory. Further investigations by Schacter and Singer (1962) suggested that bodily states must be accompanied by cognitive appraisal for an emotion to occur. However, this research did not fully resolve the basic question of the extent to which bodily states influence emotion. Recently, the James-

Lange theory was resurrected by Antonio Damasio (1994) in the form of his somatic marker hypothesis, in which feedback from the peripheral nervous system controls the *decision* about the correct behavioural response rather than the *emotional feelings* as postulated in the James-Lange theory.

An alternative to such bodily theories of emotions has been proposed by Larry Weiskrantz (1968), Jeffrey Gray (1975) and Edmund Rolls (1999) who instead regard emotions as states elicited by rewards and punishments. Emotional stimuli are evaluated and mediated by specific brain structures which subsequently give rise to feelings and to changes in bodily response.

Although the theoretical debate over the nature of emotion has been very important, the development of experimental paradigms for the reliable testing of emotion in animals and humans has had just as much influence on the field of emotion research. Given that consciousness in animals remains controversial, the presence of feelings in animals is also a contentious issue. Animals do, however, show the characteristic behavioural, autonomic and hormonal responses associated with emotional states when confronted with emotionally salient stimuli. Building on this insight, one of the most successful paradigms in emotion research has been fear *conditioning where an auditory conditioned stimulus is paired with a foot shock. LeDoux (1996) and others have shown that for rats to learn the appropriate fear response depends crucially on a brain structure in the temporal lobes called the amygdala (*Lat. almond*). Subsequently, much neuroscientific research has concentrated on elucidating the full role of the amygdala in fear, so that it has become popularly known as the fear centre in the brain. However, the amygdala is not a homogeneous brain structure but rather a collection of at least 13 anatomically distinct nuclei. In addition, other research using appetitive conditioning has also implicated the amygdala, indicating that it can be activated by both positive and negative stimuli. It is therefore unlikely that the amygdala is only concerned with fear. Nevertheless, the fear conditioning paradigm has been very successful in creating an adequate scientific model of emotion and firmly establishing the field of emotion research.

Paul Ekman's cross-cultural studies of human facial expression have been another influential paradigm which has strongly suggested an innate, biological basis for emotional experience. In the primate brain a dedicated neural circuitry for recognising faces has been found in the fusiform gyrus, and in social animals such as humans and higher primates facial expressions act as highly significant social signals communicating the state of the individual to others. Ekman's research on universally recognised facial emotions and analyses of emotion terms in all the world's major languages have led to discussions on the exis-

tence and enumeration of the fundamental emotions that can act as basic building blocks of our entire emotional repertoire. Based on such research up to seven emotions have been proposed: anger, disgust, fear, sadness, joy, shame and guilt. It remains an open question whether these emotions are really distinct or whether they are found on a continuum produced by shared brain mechanisms.

The question of what brain structures represent and mediate emotions can now be addressed more fully with *neuroimaging, which allows a unique window on the living human brain. Experimental paradigms with emotionally salient stimuli have also allowed researchers to probe the nature of emotion. Negative emotions such as fear and disgust have already been the subject of much research, while positive emotions such as joy have been found much harder to induce experimentally. Consequently only a few studies to date have dealt with this important subject. Many neuroimaging studies build on the findings from animal studies using conditioning paradigms and primary reinforcers such as taste and smell, while other studies have begun to probe the brain mechanisms involved in more complex human activities such as gambling.

The findings from neuroimaging and anatomical evidence from lesions in humans and other higher primates have pointed to the role of several interconnected brain structures in emotion. An early attempt to synthesise the emotion literature was the theory proposed by James Papez (1937) where the cingulate cortex was seen as important for the *experience* of emotion, whereas emotional *expression* was governed by the hypothalamus, and these two structures were linked by the thalamus and the hippocampus.

This theory was further elaborated by Paul MacLean (1952) with his proposal for the evolution of the triune primate brain with three functionally distinct systems, of which the limbic system was the one mediating emotion. The term limbic lobe (*Lat. limbus*, border) was proposed by Paul *Broca in 1878 who coined the name for those structures surrounding the brain stem and corpus callosum on the medial walls of the brain. Broca did not specify a specific role for the limbic lobe in emotion, and indeed subsequent research has found that the concept of emotion mediated by a unifying limbic system is too simplistic.

These early pioneering theories were built on a paucity of experimental data, and with the recent flourishing of emotion research, and especially given the ever increasing amount of human neuroimaging data, we are now in a much better position to evaluate which brain structures are crucial to emotion. The evidence points to the amygdala and the cingulate cortex as necessary for the proper emotional functioning of the primate brain. Furthermore, it has also become clear that in humans and other higher primates a very significant role is played by the orbi-

tofrontal cortex (the part of the frontal lobes just above the eyeballs). Some of the first evidence for this came from the case of the young railway engineer Phineas Gage whose medical frontal lobes were completely penetrated by a metal rod in 1848. Miraculously, he survived but his personality and emotional processing was changed completely. Recent studies have shed further light on the functioning of the orbitofrontal cortex, and shown that the reward value of primary reinforcers such as taste, smell and visual stimuli can be found there. Strong reciprocal connections are also found with the amygdala, and the scientific evidence suggests a similar role for the two brain areas, although the orbitofrontal cortex appears to be the more important for emotion in humans and higher primates.

Mood is the longer lasting continuation of an emotional state and mood disorders such as depression and anxiety affect a large proportion of the population. Some statistics suggest that as much as a third of the population will experience a major depression during their lifetime. A very important goal in understanding the neural basis of emotion is to develop better treatments for these disorders.

*Neurotransmitters acting on the frontal lobes such as serotonin, dopamine and catecholamine have all been implicated in mood disorders. This has led to the development of antidepressants that have helped many sufferers; but the efficacy of these drugs has not yet been matched by a better understanding of the underlying brain mechanisms.

There are many interesting and important issues in emotion research which are not yet fully understood. It is clear that personality plays a significant role in shaping emotions, but we are a long way from understanding personality in neural terms. Studies in *split-brain patients seems to suggest a hemispheric specialisation of emotional processing, but the issue of lateralisation is still much debated among researchers. It is also clear that although conscious appraisal of emotion is important for emotional expression, many emotional stimuli appear to be processed on a non-conscious level, only later to become available for conscious introspection (or, as in the case of *blind-sight, not at all). Emotion helps to facilitate learning and memory adaptively, and so there are strong links between emotion, learning and memory, but the exact relationship between these are not yet fully understood.

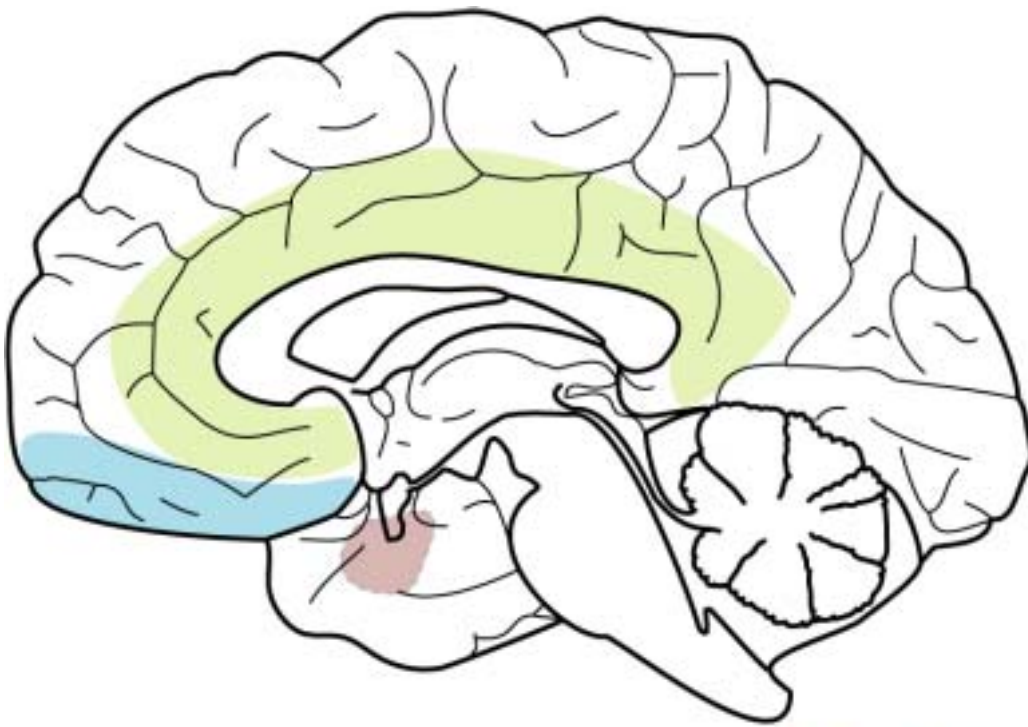
The most difficult question facing emotion research is the question of where qualia are created in the brain. Science has not yet found the neural basis for our subjective experience of emotion, and some researchers have even raised doubts about whether this will ever happen. Nevertheless, it is clear that emotions are evolutionarily important for animals in preparing for appropriate actions. The evolution of conscious feelings could be adaptive, because they




allow us to consciously appraise our emotions and actions, and subsequently to learn to manipulate these appropriately. Emotion may be one of evolution's most productive breakthroughs, constantly reminding us that we are still animals at heart, but endowed with the possibility of conscious appraisal and enhanced control of our subjective experience that comes with it.

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Fig 1. Key brain structures underlying emotion shown on a midsagittal view (top), and on a ventral view (bottom) of the human brain.



-  AMYGDALA
-  ORBITOFRONTAL CORTEX
-  CINGULATE CORTEX

