The value of life can be measured by how many times your soul has been deeply stirred.

Soichiro Honda
The beginnings of studies of emotions

Darwin’s dog, displaying the contrasting expressions of hostility and affection. From: The Expression of Emotions in Man and Animals, Charles Darwin.

Darwin first pointed out in 1872, that fearful, angry, and happy facial expressions are universal across cultures. The Expression of Emotions in Man and Animals, Charles Darwin, 1872
First theories of emotions

In early theories of emotions (James–Lange theory, Cannon-Bard theory), emotions are related to physiological reaction.

In classic James–Lange theory (1884) emotions are caused by experience of bodily responses. Alternative classic theory of Cannon and Bard (1915) proposed that emotions arise in subcortical structures (thalamus) and lead to both physiological response (mediated by the hypothalamus) and emotional experience (mediated by the cortex). Experimental support for both theories exists. For JL: Patients with the spinal cord transection, whom lack feedback from the autonomic nervous system experience a reduction in the intensity of their emotions. For CB: Despite surgically removed sympathetic nervous system the cat still displayed anger, fear and pleasure.
More recent theories of emotion

More recent theories (e.g., Schachter and Singer theory, Lazarus theory) put more emphasis on cognitive processes.

According to Schachter-Singer’s Two Factor Theory (1960) emotions depend on two factors. 1) autonomic arousal, 2) cognitive interpretation of that arousal.
In experiment confirming this theory, the participants were injected with adrenaline (which causes an increase in respiration, blood pressure and heart rate). One group was informed of the side effects, the other was not. The participants were then interacting with euphoric or angry group. The informed participants reported lower euphoria and lower anger. Another example is blind date: depending on the attitude (appraisal) one can see the autonomic arousal as positive (joy) or negative (fear).

According to cognitive appraisal theory of Lazarus (1994) thinking must occur first before experiencing emotion. Emotions arise due to initial interpretation of stimulus (appraisal) in terms of threatening or positive, relevant or irrelevant. All other components, including physiological arousal, follow the initial cognitive appraisal. Critics argue that emotional reactions to a stimulus are instantaneous – too rapid to allow for the process of cognitive appraisal. Example: somebody running towards me, when I recognize him, I felt relief.
The ‘low-road’ and ‘high-road’

Subliminal stimuli may also trigger emotions. Some emotional reactions don’t require conscious evaluation of the stimulus.

Neuroscientist Joseph LeDoux (1990) discovered a connection (so called ‘low-road’) from the thalamus to the amygdala that bypasses the cortex. It allows to process emotional stimuli rapidly without its conscious interpretation. He provides an example of fear reaction to the strike of snake in a glass cage. We first react automatically (fear reaction) and than inhibit the reaction consciously.
Joseph LeDoux - "Fear"

https://www.youtube.com/watch?v=AMI3hbgRj6o
Neurophysiology of emotion

An emotional state has two components, the one is a characteristic physical sensation and the other is a conscious feeling. The term *emotion* sometimes is used to refer only to the bodily state (i.e., the emotional state) and the term *feeling* is used to refer to conscious sensation.

Conscious feeling is mediated by the cerebral cortex, in part by the cingulate cortex and by the frontal lobes. Emotional states are mediated by a family of peripheral, autonomic, endocrine, and skeletomotor responses. These responses involve subcortical structures: the amygdala, the hypothalamus, and the brain stem.

Model of the basic neural systems that control emotions. The particular emotion experienced is a function of cross-talk between neocortical and subcortical structures, as well as feedback from peripheral receptors.
Hypothalamus integrates autonomic and somatic components of emotional behavior

Walter Cannon and Philp Bard examined behavior of cats with both cerebral hemispheres (cortex, white matter, basal ganglia) removed. The animals exhibited angry behavior with autonomous (increase of blood pressure and heart rate, dilatation of pupils, erection of the hairs on the back and tail) and somatic motor components (arching the back, extending the claws, snarling). This behavior was called sham rage (pl. fúria pozorna) because it had no obvious target. Cannon and Bard showed that transection (B) removing the forebrain and leaving the hypothalamus produced sham rage, while after transection (C) below the hypothalamus the sham rage response was lost. Additionally it was shown that electrical stimulation (A) of discrete sites in the hypothalamus of awake, freely moving cats could also lead to a rage response, and even to attack behavior.

Bard suggested that whereas the subjective experience of emotion might depend on an intact cerebral cortex, the expression of coordinated emotional behavior does not necessarily involve cortical processes.
Selective stimulation of sites in the hypothalamus may induce two basic types of attack. In affective attack (above) the animal displays sympathetic arousal, emotional excitement and rage. In quiet biting (below) the cat shows no emotion but proceeds to capture the rat and bite it.
Neural circuit underlying emotions according to Papez (1937). The loop starts with the mammillary body of the hypothalamus as the site of output for expression of the emotions (1). Collateral fibers pass to the thalamus (2) and cingulate gyrus (3). Here, it was proposed that conscious, subjective emotional experience arises. The cingulate gyrus projects to the hippocampus (4). The hippocampus integrates different inputs and projects them to the mammillary body (5).

A neural circuit for emotion extended by Paul MacLean. The circuit originally proposed by Papez is indicated by thick lines; more recently described connections are shown by fine lines. Known projections of the fornix to hypothalamic regions (mammillary bodies and other hypothalamic areas) and of the hypothalamus to the prefrontal cortex are indicated. A pathway interconnecting the amygdala to the hypothalamus is shown. Finally, reciprocal connections between the hippocampal formation and the association cortex are indicated. MacLean proposed the term limbic system.
Emotion involves entire nervous system but two especially important parts are limbic system and autonomic system. Limbic system includes: amygdala, hippocampus, hypothalamus, thalamus and cingulate gyrus.

Limbic system (Latin *limbus* – border) is a set of cortical and subcortical structures involved in emotion and formation of memories. It is functional rather than anatomical concept. Amygdala is an important structure involved in reactions to stress and anxiety but also in mediating positive emotions. It also modulates strength of memories based on emotional arousal. It is connected with many brain structures. Gets sensory inputs from the thalamus and indirectly from the cortex, which may modulate its activity. The thalamus is sorting out main features of the stimulus and speeds up the reaction. Hippocampus stores memories about events and their context and modulates amygdala activity. Hypothalamus triggers autonomic component of the emotional response. Anterior cingulate cortex mediates attentional processes and conflict monitoring in incompatible streams of information.
The amygdala

The amygdala is the part of the limbic system most specifically involved with emotional experience.

Brain imaging studies (MRI + PET + fMRI) demonstrate the role of the amygdala in emotional responses:
A. A series of faces shows a continuum of expression between happiness and fear. Activity in the brain of normal subjects was recorded as they viewed these faces.
B. With the presentation of each of the faces only the left amygdala activation was found to vary in a systematic fashion.
C. The mean regional cerebral blood flow (rCBF = PET or fMRI) shows that the responses in the amygdala were significantly greater to fearful expressions than to happy expressions. These results are consistent with ablation experiments on animals that suggest the amygdala has a critical role in emotions, particularly in fear.
The amygdala mediates both inborn and acquired emotional responses. The best studied example of a learned emotional state is the classical conditioning of fear. In this form of learning an initially neutral stimulus, such as a sound that does not evoke autonomic responses, is paired with an electric shock to the feet, which produces pain, fear, and autonomic responses. After several pairings the sound itself elicits a fearful reaction, such as freezing in place or changes in heart rate or blood pressure. Bilateral lesions of the basolateral complex of the amygdala in experimental animals abolish this learned response to fear.
Amygdala activation in affective disorders

In unipolar depression, abnormal patterns of blood flow are apparent in the “triangular” circuit interconnecting the amygdala, the mediodorsal nucleus of the thalamus, and the orbital and medial prefrontal cortex.

Areas of increased blood flow in the left amygdala, orbital, and medial prefrontal cortex (A) and in a location in the left mediodorsal thalamus (B) from a sample of patients diagnosed with unipolar clinical depression. The “hot” colors indicate statistically significant increases in blood flow, compared to a sample of nondepressed subjects. Additional active areas are: Dorsal medial prefrontal cortex (dmPFC) and Posterior cingulate cortex (PCC) belonging to Default Mode Network.
Neuronal circuits of emotions - summary

Simplified component diagram showing brain regions involved in detecting and responding to threatening sights and sounds. The figure is based primarily on work of LeDoux.

Sensory information from the senses is sent to thalamic nuclei and from there to the sensory cortex. Sensory cortex sends sensory information to the prefrontal cortex (PFC), hippocampus and amygdala. There are also connections which may send sensory information to amygdala without involvement of the cortex (blue lines).

Prefrontal cortex modulated amygdala activity (up via dorsal anterior cingulate cortex, dACC ('+') and down via ventromedial PFC, vmPFC ('-').

Hippocampus delivers contextual information to amygdala. Amygdala activates hypothalamus (paraventricular nucleus of the hypothalamus, (PVN)), which regulates autonomic nervous system (ANS) and anterior pituitary gland as well as locus coeruleus (LC) which releases noradrenaline (NA).

Cortical Lateralization of Emotional Functions

Emotionality is lateralized in the cerebral hemispheres in at least two ways. (1) The right hemisphere is in general more concerned with both the perception and expression of emotions than is the left hemisphere. The right hemisphere is especially important for the expression and comprehension of the affective aspects of speech. (2) The left hemisphere is more importantly involved with what can be thought of as positive emotions, whereas the right hemisphere is more involved with negative ones.

Asymmetrical smiles on some famous faces. Studies of normal subjects show that facial expressions are often more quickly and fully expressed by the left facial musculature than the right. The left lower face is governed by the right hemisphere, what suggests that the majority of humans are “left-faced,” in the same general sense that most of us are right-handed.
Dermal muscles of the human face as portrayed in Darwin’s book (1872). In higher mammals and especially in humans facial muscles have become adapted for the expression of emotions.
There are two anatomically and functionally distinct sets of descending projections responsible for control of the muscles of facial expression. Volitional smile is driven by the motor cortex, which communicates with the brainstem and spinal cord via the pyramidal tracts. The genuine smile is mediated by accessory motor areas in the prefrontal cortex and the basal ganglia that access brainstem nuclei via “extrapyramidal” pathways.
Comparison of human expression of smiling and laughter with bared-teeth displays of lower primates and primitive mammals. Friendly human smile evolved from more aggressive display of teeth.
Prefrontal cortical structures provide the means by which conscious thought can suppress reflex emotional responses and organize behavior.

Dorsolateral prefrontal cortex is involved in working memory and behavior planning.

Ventromedial frontal cortex is involved in emotions control and moral decisions making.

Ventrolateral prefrontal cortex (VLPFC) is engaged to stop or override motor responses.
The frontal cortices - Phineas Gage and hazard

The executive functions of behavior—judgment, long-term planning, and holding and organizing events from memory for prospective action take place in the prefrontal cortex.

The ventromedial frontal cortex is thought to provide source of cognitive control of emotional responses by predicting their consequences.

Lesions to the ventral sector of the frontal lobe result in disinhibition of inappropriate behavior in social situations.

In a “gambling experiment” a player sits draws cards from four decks of cards, labeled A, B, C, and D. He is given a loan of $2000. The undisclosed rules are that A and B cards yield $100 but occasionally require the subject to repay $1250. Cards C and D yield $50 but only require repayment of small sums (less than $100).

Normal people initially play decks A and B, but gradually, usually within 30 of the 100 trials switch to a preference for decks C and D. Patients with frontal lesions prefer cards from decks A and B throughout the test despite the high penalties and the need to borrow from the bank.
Effect of meditation on brain function and structure

In many neuroimaging studies effects of meditation practices are found to be localized in structures related to emotional control. E.g. during meditation increased activation of prefrontal cortex is observed. Also, meditation increases grey matter concentration in prefrontal cortex and insula mediating bodily self-awareness.

Stronger brain fMRI activation in the anterior cingulate cortex and medial prefrontal cortex in meditators than controls for the contrast *mindfulness vs. arithmetic.*


Frontal cortical areas are thicker in meditators.

Emotion in the body

Participants (n = 701) were shown two silhouettes of bodies alongside emotional words, stories, movies, or facial expressions. They were asked to color the bodily regions whose activity they felt increasing or decreasing while viewing each stimulus. Different emotions were consistently associated with statistically separable bodily sensation maps across experiments. These maps were concordant across West European and East Asian samples.

Participants colored the initially blank body regions (A) whose activity they felt increasing (left body) and decreasing (right body) during emotions. Individual activation–deactivation data (B) were stored and activation and deactivation maps were subsequently combined (C) for statistical analysis.
Emotion in the body

Different emotional states are associated with topographically distinct and culturally universal bodily sensations; these sensations could underlie our conscious emotional experiences.

Bodily topography of basic (Upper) and non-basic (Lower) emotions associated with words. The body maps show regions whose activation increased (warm colors) or decreased (cool colors) when feeling each emotion. From Nummenmaa et al., Bodily maps of emotions. *PNAS*, 2014, 111(2), 646-651.