



# Brain mechanisms of emotion and decision-making

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**Abstract.** Emotions can be defined as states elicited by rewarding and punishing stimuli. The thesis is being developed that brains are designed around reward and punishment evaluation systems, because this is the way that genes can build a complex system that will produce appropriate but flexible decisions to increase their fitness. Direct neurophysiological and neuroimaging evidence is being obtained that primary (unlearned and gene-specified) reinforcers such as taste, pleasant touch, pain, oral texture including viscosity and fat texture, and oral temperature are decoded and represented in the orbitofrontal cortex of primates including humans. Similarly, previously neutral stimuli such as the sight of an object become associated with primary reinforcers by rapid and reversible stimulus–reinforcement learning implemented in the orbitofrontal cortex. Neuroimaging studies in humans show that reinforcers produced by taste, smell, touch, abstract monetary reward and social reinforcers are represented in the orbitofrontal cortex, and that the orbitofrontal cortex is also activated when an expected reward is not obtained. Neuroimaging studies are also showing strong effects of cognitive inputs on representations of rewards and punishers in the orbitofrontal cortex. The human orbitofrontal cortex is further implicated in decision-making by findings that visual discrimination reversal learning, and emotional behaviour and subjective emotional experience, are impaired in humans with discrete lesions of the orbitofrontal cortex, who may also be impulsive in their decision-making. © 2006 Elsevier B.V. All rights reserved.

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## 1. Introduction

Emotions can usefully be defined as states elicited by rewards and punishments, including changes in rewards and punishments [1,2]. A reward is anything for which an animal will work. A punishment is anything that an animal will work to escape or avoid. An example of an emotion might thus be happiness produced by being given a reward,

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such as a pleasant touch, praise or winning money. Another example of an emotion might be fear produced by the sound of a rapidly approaching bus or the sight of an angry expression on someone's face. Another example would be frustration, anger or sadness produced by the omission of an expected reward. A wide range of emotions can be accounted for by incorporating not only the reinforcement contingency and intensity, but also the fact that emotions evoked by different primary (unlearned) and secondary (learned) reinforcers will be different, that any stimulus can be associated with both positive and negative reinforcers, and that the emotion elicited can depend on whether an active or passive behavioural response is possible [1].

One of the most important functions of emotion is that it allows flexibility of behavioural responses to reinforcing stimuli, in that the goals for behavior are specified by reward and punishment evaluation, and the innate goals are specified by genes. When an environmental stimulus has been decoded as a primary reward or punishment or (after previous stimulus–reinforcer association learning) as a secondary rewarding or punishing stimulus, then it becomes a goal for action. The animal can then perform any action (instrumental response) to obtain the reward, or to avoid the punisher, by action–outcome (i.e., action–reinforcement) association learning. By specifying goals and not particular actions, the genes are specifying a flexible route to action. This is in contrast to specifying a reflex response, and is also in contrast to stimulus–response, or habit, learning in which a particular response to a particular stimulus is learned.

Thus, two learning processes are involved in emotion-related decision-making. The first stage is stimulus–reinforcer association learning and the second is instrumental or action–outcome learning of a behaviour made to approach and obtain the reward or to avoid or escape from the punisher. Emotion is an integral part of this, for it is the state elicited in the first stage, by stimuli which are decoded as rewards or punishers, and this state has the property that it is motivating. The motivation is to obtain the reward or avoid the punisher, and animals must be built to obtain certain rewards and avoid certain punishers. Indeed, primary or unlearned rewards and punishers are specified by genes, which effectively specify the goals for action. This is the solution that natural selection has found for how genes can influence behaviour to promote their fitness (as measured by reproductive success) and for how the brain could interface sensory systems to action systems [1].

Selecting between available rewards with their associated costs, and avoiding punishers with their associated costs, is a process which can take place both implicitly (unconsciously) and explicitly using a language system to enable long-term plans to be made [1]. These many different brain systems, some involving implicit evaluation of rewards, and others explicit, verbal, conscious evaluation of rewards and planned long-term goals, must all enter into decision-making, and some of the brain systems involved in these types of processing are described next.

## **2. The orbitofrontal cortex**

The orbitofrontal cortex is important in emotion and decision-making because it receives taste and somatosensory information and represents the reinforcement value of these primary (unlearned) reinforcers, and rapidly learns associations between these

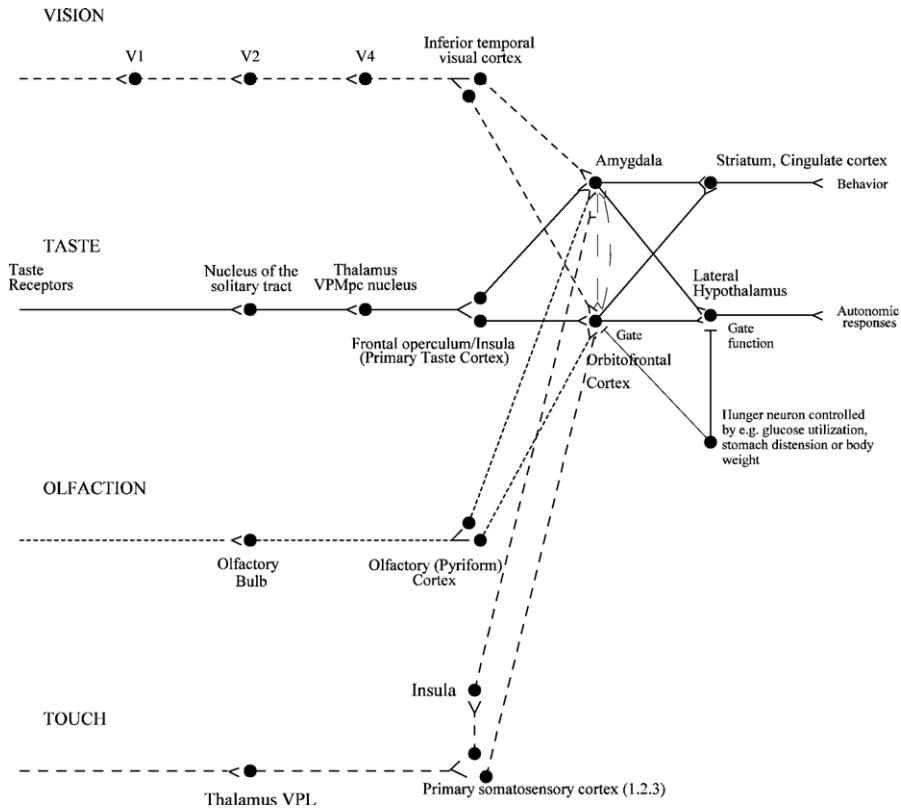


Fig. 1. Schematic diagram showing some of the gustatory, olfactory, visual and somatosensory pathways to the orbitofrontal cortex, and some of the outputs of the orbitofrontal cortex in primates. The secondary taste cortex and the secondary olfactory cortex are within the orbitofrontal cortex. V1—primary visual cortex, V4—visual cortical area V4 [2].

primary reinforcers and previously neutral visual and olfactory stimuli by stimulus–reinforcer association learning [1] (see Fig. 1).

### 2.1. Taste

The orbitofrontal cortex contains the secondary taste cortex (in that it receives inputs from the primary taste cortex in the insula) and represents tastes in terms of their reward value. This is shown by single neuron recordings in macaques indicating robust representations of the prototypical tastes sweet, salt, bitter and sour [3], but also separate representations of the “taste” of water [4], and of protein or umami as exemplified by monosodium glutamate [5,6] and inosine monophosphate [7,8]. The reward value of the taste is represented in that the responses of orbitofrontal taste neurons are modulated by hunger (as is the palatability and pleasantness of a taste) [3]. Different neurons respond unimodally to taste or multimodally to different combinations of taste, olfactory, somatosensory and visual stimuli, thus providing an information-rich and distributed representation of these sensory properties of stimuli. This allows different combinations to

be separated from each other and for sensory-specific satiety to occur to particular combinations of these sensory stimuli [1,9–13].

In human functional neuroimaging experiments (e.g., with functional magnetic resonance image, fMRI), it has also been shown that there is an orbitofrontal cortex area activated by sweet taste (glucose [14,15]) and that there are at least partly separate areas activated by the aversive taste of saline (NaCl, 0.1 M) [16], by pleasant touch [14,17] and by pleasant vs. aversive olfactory stimuli [14,18–20]. Umami (protein) taste is not only represented by neurons in the primate orbitofrontal cortex [5,7], but also human fMRI studies show that umami taste is represented in the orbitofrontal cortex, with an anterior part responding supralinearly to a combination of monosodium glutamate and inosine monophosphate [21]. Some orbitofrontal cortex neurons respond to the “taste” of water in the mouth [4], and their responses occur only when thirsty and not when satiated [3], and correspondingly in humans the pleasantness of the taste of water in the mouth is represented in the orbitofrontal cortex [22].

### *2.2. Convergence of taste and olfactory inputs in the orbitofrontal cortex: the representation of flavour*

In the orbitofrontal cortex, not only unimodal taste neurons, but also unimodal olfactory neurons are found. In addition, some single neurons respond to both gustatory and olfactory stimuli, often with correspondence between the two modalities [10]. It is probably here in the orbitofrontal cortex of primates including humans that these two modalities converge to produce the representation of flavour [10,23], for neurons in the primary taste cortex in the insular/frontal opercular cortex do not respond to olfactory (or visual) stimuli [24]. These representations are built by olfactory–gustatory association learning, an example of stimulus–reinforcer association learning, as shown below.

### *2.3. An olfactory representation in the orbitofrontal cortex*

There are neurons in the orbitofrontal cortex with olfactory responses [25] and, for many of these neurons, the odours to which they respond depend on olfactory to taste association learning [26,27]. The reward value of pleasantness of odour is represented, in that the responses of many of these neurons only occur to a food-related odour if hunger is present [28], and indeed these neuronal responses parallel the changes in the relative pleasantness of different foods after a food is eaten to satiety [1] (see [2,19,29 30 31]). Correspondingly, in humans, the orbitofrontal cortex is activated by odours [32,33], and the reward or affective value is represented in that the human medial orbitofrontal cortex has activation that is related to the subjective pleasantness of a set of odours, and a more lateral area has activation that is related to how unpleasant odours are subjectively [20]. Moreover, the pleasantness or reward value of odour is represented in the orbitofrontal cortex, in that feeding the humans to satiety decreases the activation found to the odour of that food and this effect is relatively specific to the food eaten in the meal [14,18].

An fMRI study has shown that cognitive effects can reach down into the human orbitofrontal cortex and influence activations produced by odours [34]. In this study, a standard test odour, isovaleric acid with a small amount of cheese flavour, was delivered through an olfactometer. (The odour alone, like the odour of brie, might have been interpreted as pleasant or perhaps as unpleasant.) On some trials, the test odour was

accompanied with the visually presented word label “Cheddar cheese” and on other trials with the word label “body odour”. It was found that the activation in the medial orbitofrontal cortex to the standard test odour was much greater when the word label was Cheddar cheese than when it was body odour. (Controls with clean air were run to show that the effect could not be accounted for by the word label alone.) Moreover, the word labels influenced the subjective pleasantness ratings to the test odour and the changing pleasantness ratings were correlated with the activations in the human medial orbitofrontal cortex. Part of the interest and importance of this finding is that it shows that cognitive influences, originating here purely at the word level, can reach down and modulate activations in the first stage of cortical processing that represents the affective value of sensory stimuli [1,34].

#### *2.4. Visual inputs to the orbitofrontal cortex, error detection neurons, visual stimulus–reinforcement association learning and reversal, and neurons with face-selective responses*

We have been able to show that there is a major visual input to many neurons in the orbitofrontal cortex and that what is represented by these neurons is in many cases the reinforcement association of visual stimuli. The visual input is from the ventral, temporal lobe, visual stream concerned with “what” object is being seen (see Refs. [35,36]). Using this object-related information, orbitofrontal cortex visual neurons frequently respond differentially to objects or images depending on their (taste) reward association, and learn and reverse these associations in one or a very few trials [27,37]. The probable mechanism for this learning is an associative modification of synapses conveying visual input onto taste-responsive neurons, implementing a pattern association network [2,36,38]. To implement one-trial reversal, conditional reward neurons (which respond only to some objects and only if they are associated with reward) may be biased on by rule neurons in a rule attractor network, which itself can be reversed by error neurons [39]. The reward value of the sight of food is what is represented, in that the majority of these neurons gradually stop responding to the sight of a food that is fed to satiety [28].

In addition to these neurons that encode the reward association of visual stimuli, other, “error”, neurons in the orbitofrontal cortex detect non-reward, in that they respond for example when an expected reward is not obtained when a visual discrimination task is reversed [37].

There are also neurons in the orbitofrontal cortex that respond to the sight of faces, with some tuned to identity, and thus potentially being involved in stimulus–reinforcer association learning and others tuned to face expression or movement, and thus potentially involved in signalling reinforcement [40].

Correspondingly, in humans, there is a part of the orbitofrontal cortex that responds selectively in relation to face expression specifically when it indicates that behaviour should change and this activation is error-related [41]. Further, there are impairments in the identification of facial and vocal emotional expression in a group of patients with ventral frontal lobe damage who have socially inappropriate behaviour [42,43].

### 2.5. Somatosensory inputs to the orbitofrontal cortex

Somatosensory sensory inputs, which can act as primary reinforcers, also reach the orbitofrontal cortex, in that some neurons respond to oral fat texture, to oral viscosity and to oral temperature [9,11–13,44]. In a complementary human fMRI study, it has been shown that activation of parts of the orbitofrontal cortex, primary taste cortex and mid-insular somatosensory region posterior to the insular taste cortex have activations that are related to the viscosity of what is in the mouth, and that there is in addition a medial prefrontal/cingulate area where the mouth feel of fat is represented [45].

In addition to these oral somatosensory inputs to the orbitofrontal cortex, there are also somatosensory inputs from other parts of the body, and indeed an fMRI investigation we have performed in humans indicates that pleasant and painful touch stimuli to the hand produce greater activation of the orbitofrontal cortex relative to the somatosensory cortex than do affectively neutral stimuli [14,17].

### 2.6. Functions of the orbitofrontal cortex in emotion and decision-making

These findings in macaques and humans show that the orbitofrontal cortex is important in emotion and decision-making because it receives taste and somatosensory information and represents the reinforcement value of these primary (unlearned) reinforcers, and rapidly learns associations between these primary reinforcers and previously neutral visual and olfactory stimuli by stimulus–reinforcer association learning [1] (see Fig. 1). Damage to the orbitofrontal cortex impairs emotional behaviour particularly when it must change when reinforcement contingencies alter so that new decisions must be made and indeed patients with damage to the orbitofrontal cortex are impulsive [1,42,43,46–49].

## 3. The amygdala

Although the amygdala is concerned with some of the same functions as the orbitofrontal cortex and receives similar inputs (see Fig. 1), there is evidence that it may function less effectively in the very rapid learning and reversal of stimulus reinforcement associations, as indicated by the greater difficulty in obtaining reversal from amygdala neurons (see Refs. 50–52) and by the greater effect of orbitofrontal lesions in leading to continuing choice of no longer rewarded stimuli [53]. In primates, the necessity for very rapid stimulus-reinforcement re-evaluation and the development of powerful cortical learning systems may result in the orbitofrontal cortex effectively taking over this aspect of amygdala functions (see Refs. [1,2,50]).

## 4. The anterior cingulate cortex

The anterior cingulate cortex receives inputs from the orbitofrontal cortex and may provide a site for the reinforcing outcomes to influence the actions selected [1,54,55]. Patients with anterior cingulate damage have some impairments in emotion [43].

## 5. Emotion and decision-making

I have shown above how rewards and punishers provide a basis for understanding emotion. Rewards and punishers, and emotion, are important in decision-making. I now summarize how there are different types of choice or decision that are made about rewards and punishers, and how emotion is related to these different types of decision [1].

### 5.1. *Selection of mainly autonomic responses and their classical conditioning*

Responses produced by primary rewards and punishers, such as salivation, a change of heart rate or arousal, can become classically conditioned (see Ref. [1]) and this is a form of stimulus-response (conditioned stimulus–unconditioned response) learning. These responses are important for fitness, and are being selected, but hardly merit the term ‘decision’. Brain regions such as the amygdala, orbitofrontal cortex and anterior cingulate cortex are involved in these responses [1].

### 5.2. *Selection of approach or withdrawal, and their classical conditioning*

Rewards and punishers also lead to approach or withdrawal, and these effects can be classically conditioned [1]. This is an important way in which genes can influence the behaviour that is selected and this might be thought of as a very simple, automated, ‘decision’. However, there is little flexibility in the response that is selected, in that the behaviour is either approach (e.g., to a sweet taste) or withdrawal/rejection (e.g., to a bitter taste), and in this sense behaviour is being selected by the reinforcer, but the ‘decision’ is essentially an automated type of behaviour. This type of approach behaviour to rewards can be classically conditioned, resulting in conditioned ‘incentive salience’ or ‘wanting’ effects [56,57], and this learning is implemented via the amygdala and ventral striatum, is under control of dopamine [54] and contributes to addiction [58].

### 5.3. *Selection of fixed stimulus-response habits*

Stimulus-response connections can be reinforced by rewards or punishers to produce fixed habits [1]. Habits typically arise when behavioural responses are overlearned and it is suggested that action–outcome learning sets up the correct stimulus-response conditions for a habit learning system to implement fixed responses to stimuli [1]. Once a habit has been learned, we may think of the behavioural selection as being a rather fixed type of ‘decision’. The basal ganglia may be especially involved in habit learning [1], and they do receive inputs that may be important in this process from the amygdala and orbitofrontal cortex. Reinforcement learning (see below) using reward prediction errors implemented in dopamine neuron firing may or not be important in this habit learning [1,59–62].

### 5.4. *Selection of arbitrary behaviours to obtain goals, action–outcome learning and emotional learning*

The real power of emotion, and rewards and punishers, occurs when goals for actions are specified by genes, and arbitrary actions can then be performed (instrumentally) to

achieve the goals (see Chapters 2 and 3 of Rolls [1]). The type of learning involved is action–outcome learning (see Chapter 4 of Rolls [1]). Motivated behaviour is made to obtain, terminate or avoid the goal, and when the reward or punisher is or is not obtained, terminated or avoided, emotional states occur that may be further motivating.

The orbitofrontal cortex is important in representing the rewards and punishers, and in performing rapid stimulus–reinforcer association learning and reversal. This is the fundamental type of learning involved in producing learned emotional or affective states and is stimulus–stimulus learning. The orbitofrontal cortex is not itself involved in action–outcome association learning, in that actions appear not to be represented in the orbitofrontal cortex [1]. It is important for action–outcome learning though, in that it represents the affective outcomes. Brain regions such as the cingulate cortex may be involved in action–outcome association learning [1], and receive inputs about the outcomes, and predicted outcomes, from the orbitofrontal cortex.

### 5.5. *The roles of the prefrontal cortex in decision-making and attention*

The dorsolateral prefrontal cortex is involved in short-term memory, and this functionality enables it to participate in certain types of decision-making, those decision tasks that require a short-term or working memory, and in which biased competition provides a decision mechanism [1,36,63–66].

### 5.6. *Neuroeconomics, reward value and expected utility*

The question arises of how a decision is influenced if the reward magnitude is high, but there is a small probability of obtaining the reward. We can adopt approaches used in microeconomics and define the *reward value* as the magnitude of the reward, and the *expected utility* as approximating the probability of obtaining the reward multiplied by the reward value [67–69]. (The approximation is that, in some circumstances, humans behave somewhat differently from this specification, being for example more risk averse than the above formulation would indicate [69].) Correlates of expected utility have been found in a number of brain areas, including the parietal cortex, cingulate cortex and the superior colliculus [70].

Another factor that can influence decisions for rewards is the delay before the reward is obtained. If the reward will not be available for a long time, then we discount the reward value. Most models assume an exponential decrease in the reward value as a function of the delay until the reward is obtained, as rational choice entails treating each moment of delay equally [71,72]. It is possible that there are two systems that influence decisions in these circumstances, a rational, logic-based, system requiring syntactic manipulation of symbols and a more emotion-based system [1].

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