Chapter 12
Evolution of the Emotional Brain

Edmund T. Rolls

Abstract The brain systems and processing involved in emotion in vertebrates have evolved considerably. The way in which the primate orbitofrontal cortex has undergone great evolutionary development in primates and comes to overshadow the much evolutionarily older amygdala for many functions related to emotion is described. Indeed there may be no cortical area in rodents that is homologous to most of the primate including human orbitofrontal cortex. The primate including human orbitofrontal cortex (OFC) implements reward value. Value is not represented at earlier stages of processing in primates including humans. Invariant visual object recognition is used for many functions including memory formation, so perception is kept separate from emotion. In contrast, in rodents, value is represented even in the first taste relay in the brain, the nucleus of the solitary tract: there is no clear separation between perception and emotion. In rodents, even the taste pathways are connected differently, with subcortical connections bypassing the cortex (including orbitofrontal cortex) and making connections via a pontine taste area directly to the hypothalamus and amygdala. Goal value-directed choice is usual in primates and humans, whereas fixed action patterns, such as pecking in birds, are more common elsewhere. In humans, and perhaps some primates, syntactic reasoning and thereby planning allows selfish gene-specified (emotion-related) rewards to be rejected in favour of the long-term interests of the individual, the phenotype.

Keywords Emotion • Evolution of emotion • Orbitofrontal cortex • Amygdala • Value • Reward

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12.1 Introduction

The brain systems and processing involved in emotion in vertebrates have evolved considerably. Some of the principles that I elucidate in this chapter include the following (Rolls 2014):

1. The primate orbitofrontal cortex has undergone great evolutionary development in primates and comes to overshadow the much evolutionarily older amygdala for many functions related to emotion. Indeed there may be no cortical area in rodents that is homologous to most of the primates including human orbitofrontal cortex.
2. The primate including human orbitofrontal cortex (OFC) implements reward value, as shown by devaluation experiments such as feeding to satiety.
3. Value is not represented at earlier stages of processing in primates including humans. Invariant visual object recognition is used for many functions including memory formation, so perception is kept separate from emotion.
4. In contrast, in rodents, value is represented even in the first taste relay in the brain, the nucleus of the solitary tract: there is no clear separation between perception and emotion. In rodents, even the taste pathways are connected differently, with subcortical connections bypassing the cortex (including orbitofrontal cortex) and making connections via a pontine taste area directly to the hypothalamus and amygdala.
5. In primates and humans, the orbitofrontal cortex implements one-trial rule-based reversal learning, and this is important in rapidly updating social behaviour. This is rapid updating of value-based representations. Maintaining the current rule in short-term memory and using this to bias neurons in the orbitofrontal cortex may be one computation that granular prefrontal cortex facilitates. Rodents may not be able to perform this.
6. The value representation in the primate and human orbitofrontal cortex is domain general, in that the amount and value of goods, and temporal discounting, operate transitively (as shown by trade-offs), providing a basis for economic decision-making. There is evidence that this is not the case in rodents.
7. Goal-directed choice may be the best measure of value and emotion, for there are many partly separate neural circuits for different emotion-related responses, e.g. autonomic output, freezing, fixed action patterns, and unconditioned approach or withdrawal.
8. Goal value-directed choice is usual in primates and humans, whereas fixed action patterns, such as pecking in birds, are more common elsewhere.
9. In humans, and perhaps some primates, syntactic reasoning and thereby planning allows selfish gene-specified (emotion-related) rewards to be rejected in favour of the long-term interests of the individual, the phenotype.

These principles are now elucidated.

12.2 An Anatomical and Functional Framework for Understanding the Neural Basis of Emotion

Emotions can be defined as states elicited by rewards and punishers, that is, by instrumental reinforcers, which are the goals for action (Rolls 2013, 2014, 2015b, 2016a). Motivational states can be defined as states in which an instrumental reinforcer is the goal for action (Rolls 2016b). The principle of operation is that genes can specify goals for actions that are in the selfish interests of the genes. By specifying the rewards (e.g. a sweet taste) and punishers (e.g. painful touch), the specification is simpler than trying to specify detailed behavioural responses to stimuli and allows much greater flexibility of the actions, which can be learned instead of prespecified by the genes. Emotions are states that can continue after the eliciting stimulus is no longer present, for example, when an expected reward is not obtained, and this is adaptive, for the state can influence ongoing goal directed behaviour, for example, to obtain a missing reward. The approach to emotions that I have described, as states elicited by (instrumental) rewards and punishers, relates emotions to goals and is therefore different from measuring emotion by respondents such as autonomic responses to unconditioned approach or flight. Indeed, a rich set of mechanisms are brought into play when rewards and punishers are delivered, and one must be very careful to distinguish the different types of mechanism involved, as set out in section 4.6.1 (pp. 159–165) of Emotion and Decision-Making Explained (Rolls 2014) and by Cardinal et al. (2002).

I now provide a framework for understanding some of the brain structures involved in emotion in primates including humans and at the same time contrast them with the structures that in terms of connectivity and function precede them and succeed them in the anatomical and functional hierarchy moving from left to right in Fig. 12.1 (Rolls 2014). This provides a framework within which to consider the evolution of these systems involved in emotion. In line with the definition of emotion provided above, the interest is in the brain systems that compute and represent reward value and then provide this as an input to decision and action systems.

In Tier 1 of Fig. 12.1, information is processed to a level at which the neurons represent ‘what’ the stimulus is, independently of the reward or punishment value of the stimulus. Thus neurons in the primary taste cortex represent what the taste is, and its intensity, but not its reward value (Rolls 2014). In the inferior temporal visual cortex, the representation is of objects, invariantly with respect to the exact position on the retina, size, and even view. Forming invariant representations involves a great deal of cortical computation in the hierarchy of visual cortical areas from the primary visual cortex V1 to the inferior temporal visual cortex (Rolls 2012a, 2016a). The fundamental advantage of this separation of ‘what’ processing in Tier 1 from reward value processing in Tier 2 is that any learning in Tier 2 of the value of an object or face seen in one location on the retina, size, and view will generalize to other views, etc. In rodents, there is no such clear separation of ‘what’ from ‘value’ representations. For example, in the taste system, satiety

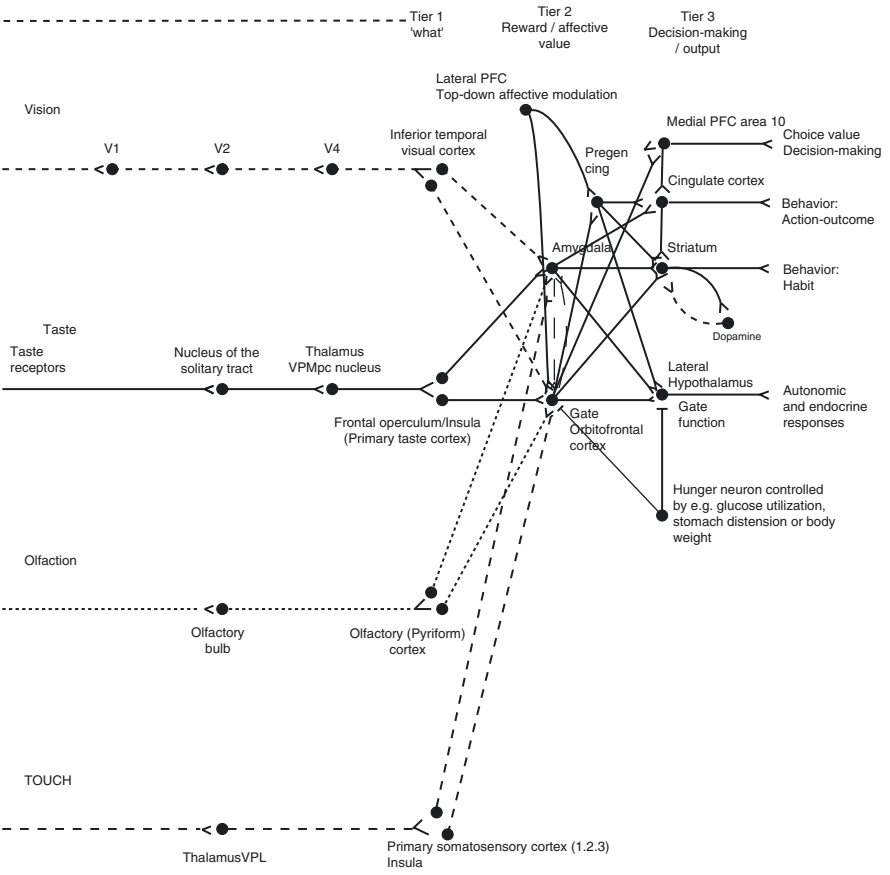

Fig. 12.1 Schematic diagram showing some of the gustatory, olfactory, visual, and somatosensory pathways to the orbitofrontal cortex, and some of the outputs of the orbitofrontal cortex, in primates. The secondary taste cortex and the secondary olfactory cortex are within the orbitofrontal cortex. V1—primary visual cortex. V4—visual cortical area V4. PreGen Cing—pregenual cingulate cortex. 'Gate' refers to the finding that inputs such as the taste, smell, and sight of food in some brain regions only produce effects when hunger is present (Rolls 2014). Tier 1: the column of brain regions including and below the inferior temporal visual cortex represents brain regions in which 'what' stimulus is present is made explicit in the neuronal representation, but not its reward or affective value which are represented in the next tier of brain regions (Tier 2), the orbitofrontal cortex and amygdala, and in the anterior cingulate cortex. In Tier 3 areas beyond these such as medial prefrontal cortex area 10, choices, or decisions about reward value are taken (Rolls 2008b, 2014; Rolls and Deco 2010). Top-down control of affective response systems by cognition and by selective attention from the dorsolateral prefrontal cortex is also indicated. Medial PFC area 10—medial prefrontal cortex area 10; VPMpc—ventralposteromedial thalamic nucleus, the thalamic nucleus for taste

influences taste processing at the first central synapse in the taste system (Rolls and Scott 2003), and this property makes the processing in rodents not only different from that in primates including humans but also much more difficult to analyse (Rolls 2014, 2015a).

In Tier 2 of Fig. 12.1, there are brain mechanisms in the orbitofrontal cortex that are involved in computing the reward value of primary (unlearned) reinforcers, as shown by devaluation experiments in which, for example, a food is fed to satiety (Rolls et al. 1989; Critchley and Rolls 1996a; Kringelbach et al. 2003; Rolls and Grabenhorst 2008), and by neuroeconomics experiments which show that the amount and quality of each commodity is encoded by orbitofrontal cortex neurons (Padoa-Schioppa 2011; Padoa-Schioppa and Assad 2008; Grabenhorst and Rolls 2011). The primary reinforcers include taste, touch (both pleasant touch and pain), and to some extent smell, and perhaps certain visual stimuli such as face expression. There is evidence that there is a representation of the (reward/punishment) value of many primary reinforcers in the orbitofrontal cortex, including taste, positive touch and pain, face expression, face beauty, and auditory consonance/dissonance. In neuroeconomics, these are termed 'outcome value' representations (Rolls 2014). Further evidence for value representations is that orbitofrontal cortex activations in humans to these stimuli are linearly related to the subjectively reported pleasantness of stimuli (medially) or to their unpleasantness (laterally) (Rolls 2014).

Brain regions in Tier 2 are also concerned with learning associations between previously neutral stimuli, such as the sight of objects or of individuals' faces, with primary reinforcers. These brain regions include the amygdala and orbitofrontal cortex, with the orbitofrontal cortex being especially important in the rapid, one-trial learning and reversal of stimulus-reinforcer associations. In neuroeconomics, these are termed 'expected value' representations. Once the Tier 2 brain regions have determined whether the input is reinforcing, whether primary or secondary, the signal is passed directly to output regions of the brain, with no need to produce and then feedback peripheral body or autonomic responses to the brain.

In Tier 2 in the orbitofrontal cortex, the representation is of the value of stimuli, and actions are not represented. The value of very many different types of stimuli, events, or goals is represented separately at the neuronal level, providing the basis for choice between stimuli and the selection at later stages of processing of an appropriate action to obtain the chosen goal.

In Tier 3, the medial prefrontal cortex area 10/ventromedial prefrontal cortex is implicated in decision-making between stimuli, in which a selection or choice must be made, moving beyond a representation of value on a continuous scale towards a decision between goods based on their value (Rolls 2014; Grabenhorst et al. 2011; Rolls et al. 2008).

The Tier 2 brain regions in which the reinforcing, and hence emotional, value of stimuli is represented in primates include mainly the orbitofrontal cortex and amygdala, which interface to three other main types of output system in Tier 3 (Figs. 12.1 and 12.2):

In Tier 3, the first is the autonomic and endocrine system, for producing such changes as increased heart rate and release of adrenaline, which prepare the body for action. Structures receiving from the orbitofrontal cortex, amygdala, and anterior cingulate cortex that provide a route for these autonomic effects include the hypothalamus and parts of the anterior insula close to the insular taste cortex (Rolls 2014; Critchley and Harrison 2013).

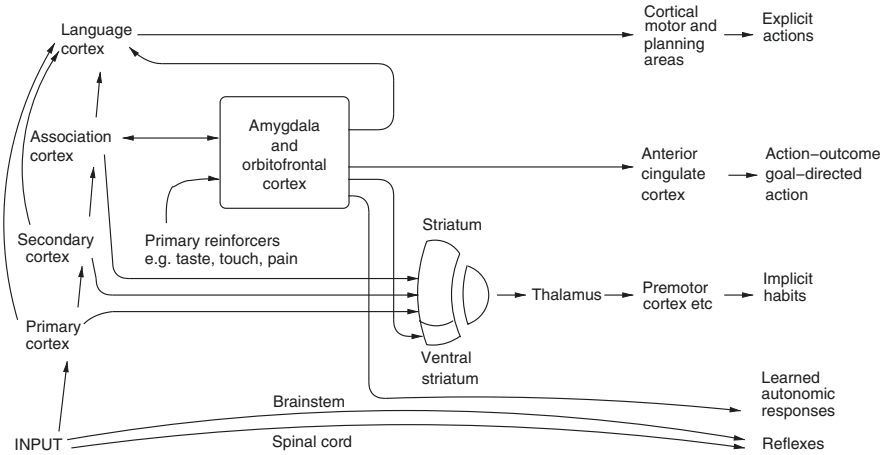

Fig. 12.2 Dual routes to the initiation of actions in response to rewarding and punishing stimuli. The inputs from different sensory systems to brain structures such as the orbitofrontal cortex and amygdala allow these brain structures to evaluate the reward- or punishment-related value of incoming stimuli, or of remembered stimuli. One type of route is via the language systems of the brain, which allow explicit (verbalizable) decisions involving multistep syntactic planning to be implemented. The other type of route may be implicit and includes the anterior cingulate cortex for action-outcome, goal-dependent learning and the striatum and rest of the basal ganglia for stimulus-response habits. The basal ganglia may be involved in selecting only one system for output. Outputs for autonomic responses can also be produced using outputs from the orbitofrontal cortex and anterior cingulate cortex (some of which are routed via the anterior insular cortex) and amygdala

The second type of output is to brain systems concerned with performing actions unconsciously or implicitly, in order to obtain rewards or avoid punishers. One of these brain systems is the basal ganglia for habit ('stimulus-response') behaviour, in which the behaviour becomes no longer under the control of the goal as shown by devaluation procedures but is a stimulus-to-motor-response association, which are necessary strong emotional states (Rolls 2014). A second brain system is the anterior cingulate cortex for goal-directed, action-outcome learning (Rolls 2014). (The 'outcome' is the reward or punisher that is or is not obtained when the action is performed to obtain the goal.) The anterior cingulate cortex contains representations of reward and punisher value, and thus of outcome, which are essential for learning associations between actions and the outcomes that follow actions. The mid-cingulate area contains representations of actions.

The third type of output in humans and perhaps related animals is to a system capable of planning many steps ahead and, for example, deferring short-term rewards in order to execute a long-term plan. This system may use syntactic processing to perform the planning and is therefore part of a linguistic system which performs explicit (conscious) processing, as described more fully elsewhere (Rolls 2014).

12.3 Evolution of the Primate Orbitofrontal Cortex

Many of the brain systems that are involved in emotion have undergone considerable development in primates (e.g. monkeys and humans) (Rolls 2014), as summarized next.

First, the temporal lobe has undergone great development in primates, and several systems in the temporal lobe are either involved in emotion (e.g. the amygdala) or provide some of the main sensory inputs to brain systems involved in emotion and motivation. For example, the amygdala and the orbitofrontal cortex, key brain structures in emotion, both receive inputs from the highly developed primate temporal lobe cortical areas, including those involved in invariant visual object recognition and face identity and expression processing (Rolls 2000, 2011, 2012a, 2014).

Second, the prefrontal cortex has undergone great development in primates, and one part of the prefrontal cortex, the orbitofrontal cortex, is very little developed in rodents yet is one of the major brain areas involved in emotion, motivation, and reward value processing including for taste, olfactory, and visual inputs in primates including humans. With this great development of the orbitofrontal cortex in primates, there may be division of functionality, with the primate taste insula not performing taste-related hedonic functions (Rolls 2015c). Indeed, it has been argued (on the basis of cytoarchitecture, connections, and functions) that the granular prefrontal cortex is a primate innovation (Preuss 1995; Wise 2008; Passingham and Wise 2012; Rolls 2014, 2015c), and the implication of the argument is that any areas that might be termed orbitofrontal cortex in rats (Schoenbaum et al. 2009) are homologous only to the agranular parts of the primate orbitofrontal cortex, that is, to areas 13a, 14c, and the agranular insular areas Ia (Passingham and Wise 2012) (shaded mid grey in Fig. 12.3). Indeed, there may be no cortical area in rodents that is homologous to most of the primates' including human orbitofrontal cortex (Preuss 1995; Wise 2008; Passingham and Wise 2012; Rolls 2014, 2015c). It follows from that argument that for most areas of the orbitofrontal and medial prefrontal cortex in humans and macaques (those shaded light grey in Fig. 12.3), special consideration must be given to research in macaques and humans.

Third, even the taste system (which might have been supposed to be phylogenetically old and preserved) of primates and rodents may be different, with obligatory processing from the nucleus of the solitary tract via the thalamus to the cortex in primates, but a subcortical pathway in rodents via a pontine taste area to the amygdala, and differences in where satiety influences taste-responsive neurons in primates and rodents (Norgren 1984; Rolls and Scott 2003; Small and Scott 2009; Rolls 2014, 2015a).

Fourth, with the great development of the orbitofrontal cortex in primates, the amygdala may become relatively less important in humans in emotion than in other vertebrates (Rolls 2014).

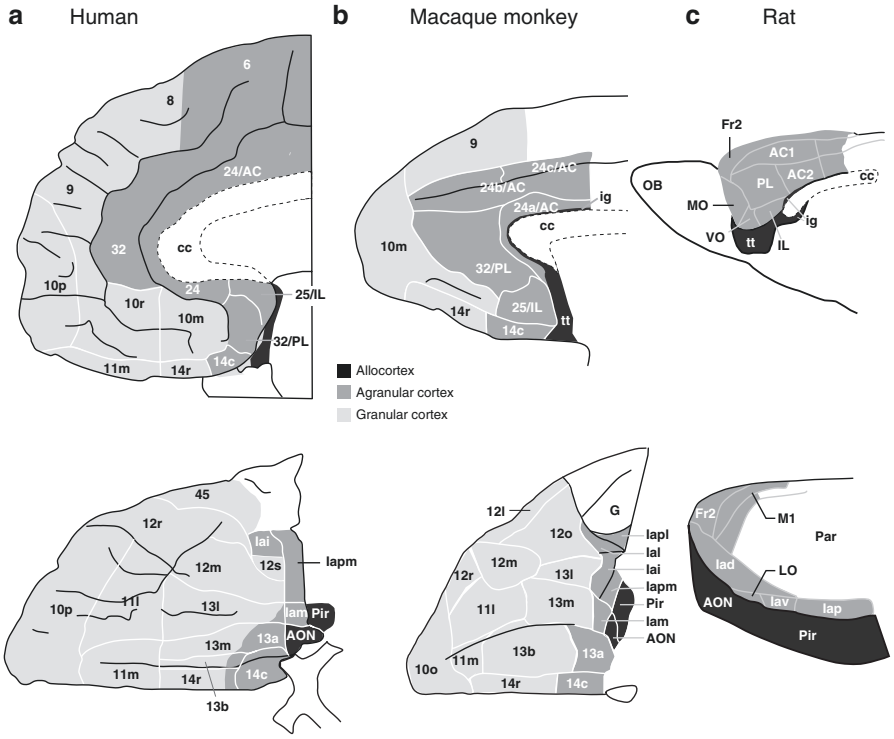

Fig. 12.3 Comparison of the orbitofrontal (below) and medial prefrontal (above) cortical areas in humans, macaque monkeys, and rats. (**a**) Medial (*top*) and orbital (*bottom*) areas of the human frontal codex (Ongur et al. 2003). (**b**) Medial (*top*) and orbital (*bottom*) areas of the macaque frontal cortex (Carmichael and Price 1994). (**c**) Medial (*top*) and lateral (*bottom*) areas of rat frontal cortex (Palomero-Gallagher and Zilles 2004). Rostral is to the *left* in all drawings. *Top row*: dorsal is up in all drawings. *Bottom row*: in (**a**, **b**), lateral is up; in (**c**), dorsal is up. Not to scale. Abbreviations: *AC* anterior cingulate cortex, *AON* anterior olfactory 'nucleus', *cc* corpus callosum, *Fr2* second frontal area, *Ia* agranular insular cortex, *ig* indusium griseum, *IL* infralimbic cortex, *LO* lateral orbital cortex, *MO* medial orbital cortex, *OB* olfactory bulb, *Pr* piriform (olfactory) cortex, *PL* prelimbic cortex, *tt* tenia tecta, *VO* ventral orbital cortex; Subdivisions of areas are labelled caudal (c), inferior (i), lateral (l), medial (m), orbital (o), posterior or polar (p), rostral(r), or by arbitrary designation (a, b) (After Passingham and Wise (2012). (**a**) Adapted from Dost Ongur, Amon T. Ferry, and Joseph L. Price, Architectonic subdivision of the human orbital and medial prefrontal cortex, Journal of Comparative Neurology, 460 (3), pp. 425–49 Copyright 2003 Wiley-Liss, Inc. (**b**) Adapted from S. T. Carmichael and J. L. Price, Architectonic subdivision of the orbital and medial prefrontal cortex in the macaque monkey, Journal of Comparative Neurology, 346 (3), pp. 366–402 Copyright 1994 Wiley-Liss, Inc. (**c**) Adapted from Palomero-Gallagher N. and Zilles K., Isocortex, in The Rat Nervous System 3rd edn. G. Paxinos, pp. 729–57 Copyright 2004, Elsevier Academic Press

12.4 The Primate Including Human Orbitofrontal Cortex (OFC) Implements Reward Value

Let us start with the reward value of taste, which can be measured in devaluation experiments such as feeding to satiety, which decreases food reward value, and in humans the pleasantness of food, to zero. In the macaque orbitofrontal cortex throughout its mediolateral extent, almost all neurons show a decrease to zero of the response to taste, that is, the neurons do not alter from their spontaneous firing rate, after feeding to satiety (Rolls et al. 1989; Critchley and Rolls 1996a; Pritchard et al. 2008; Rolls 2015c). Similar effects are found for fat texture (Rolls et al. 1999; Verhagen et al. 2003). In the human orbitofrontal cortex, we found a large decrease in the BOLD signal to a complex food (tomato juice vs. chocolate) fed to satiety, but not in the insula (Kringelbach et al. 2003). Moreover, this was a sensory-specific decrease in the BOLD signal, a useful indication that this was a response related to real satiety, which is to a considerable extent sensory-specific, and not for every food (Rolls 2016d). Moreover, this sensory-specific decrease was related to the decrease in the subjective pleasantness of the food eaten to satiety. Further, we are looking for a brain region not just where there may be small changes to the response to a taste fed to satiety, but a region where the response decreases to zero, for this is what happens to the pleasantness of food after it is fed to satiety, with little effect on its intensity (Rolls et al. 1983; Rolls and Grabenhorst 2008; Rolls 2014). A detailed analysis of the functions of different parts of the primate including human anterior insula in taste and related functions is provided elsewhere (Rolls 2015a).

Odours are also represented in the macaque orbitofrontal cortex (Critchley and Rolls 1996b; Rolls et al. 1996b). It was shown that the majority of orbitofrontal olfactory neurons decrease their responses to the odour of the food with which the monkey was fed to satiety (Critchley and Rolls 1996a). The subjective pleasantness or reward or affective value of odour is represented in the orbitofrontal cortex, in that feeding 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 (Francis et al. 1999; O'Doherty et al. 2000; cf. Morris and Dolan 2001). Further, 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 the degree of subjective unpleasantness of odours (Rolls et al. 2003). An fMRI investigation in humans showed that whereas in the orbitofrontal cortex the pleasantness vs. unpleasantness of odours is represented, this was not the case in primary olfactory cortical areas, where instead the activations reflected the intensity of the odours (Rolls et al. 2003).

There is a major visual input to many neurons in the orbitofrontal cortex, and what is represented by these neurons is in many cases the reinforcement association of visual stimuli, i.e. their reward/punishment value. The visual input is from the ventral, temporal lobe, visual stream concerned with 'what' object is being seen (see Rolls 2000, 2012a, 2016a). Many neurons in these temporal cortex visual areas have responses to objects or faces that are invariant with respect to size, position on the retina, and even view (Rolls 2000, 2007, 2008a, b, 2009, 2012a, 2016a), making these neurons ideal as an input to a system that may learn about the reinforcement association properties of objects and faces, for after a single learning trial, the learning then generalizes correctly to other views, etc. (see Rolls 2000, 2008b, 2012a, 2014, 2016a). Using this object-related information, orbitofrontal cortex visual neurons frequently respond differentially to objects or images depending on their reward association (Thorpe et al. 1983; Rolls et al. 1996b). The primary reinforcer that has been used is taste, and correlates of visual to taste association learning have been demonstrated in the human orbitofrontal cortex with fMRI (O'Doherty et al. 2002). Many of these neurons show visual-taste reversal in one or a very few trials. (In a visual discrimination task, they will reverse the stimulus to which they respond, from e.g. a triangle to a square, in one trial when the taste delivered for a behavioural response to that stimulus is reversed (Thorpe et al. 1983).) This reversal learning probably occurs in the orbitofrontal cortex, for it does not occur one synapse earlier in the visual inferior temporal cortex (Rolls et al. 1977), and it is in the orbitofrontal cortex that there is convergence of visual and taste pathways onto the same single neurons (Thorpe et al. 1983; Rolls and Baylis 1994; Rolls et al. 1996b). Moreover the majority of orbitofrontal visual food-related neurons decrease their responses to the sight of the food with which the monkey was fed to satiety. Thus for these neurons, the expected reward value of the sight of food is what is represented in the orbitofrontal cortex (Critchley and Rolls 1996a).

Another type of visual information represented in the orbitofrontal cortex that is relevant to emotion is information about faces. There is a population of orbitofrontal cortex neurons that respond in many ways similarly to those in the temporal cortical visual areas (Rolls 1984, 1992, 1996, 2000, 2007; Rolls and Deco 2002). The orbitofrontal cortex face-responsive neurons, first observed by Thorpe et al. (1983), then by Rolls et al. (2006), tend to respond with longer latencies than temporal lobe neurons (140–200 ms typically, compared to 80–100 ms); also convey information about which face is being seen, by having different responses to different faces; and are typically rather harder to activate strongly than temporal cortical face-selective neurons, in that many of them respond much better to real faces than to two-dimensional images of faces on a video monitor (Rolls et al. 2006; Rolls 2011) (cf. Rolls and Baylis 1986). Some of the orbitofrontal cortex face-selective neurons are responsive to face expression, gesture, or movement (Rolls et al. 2006). The findings are consistent with the likelihood that these neurons are activated via the inputs from the temporal cortical visual areas in which face-selective neurons are found (see Fig. 12.1). The significance of the neurons is likely to be related to the fact that faces convey information that is important in social reinforcement in at least two

ways that could be implemented by these neurons. The first is that some may encode face expression (Rolls et al. 2006) (cf. Hasselmo et al. 1989), which can indicate reinforcement. The second way is that they encode information about which individual is present (Rolls et al. 2006), which by stimulus-reinforcement association learning is important in evaluating and utilizing learned reinforcing inputs in social situations, e.g. about the current reinforcement value as decoded by stimulus-reinforcement association, to a particular individual. Between them, these neurons represent whose face has a particular expression, and this is important in social situations. This system is likely to be a primate specialization, made possible by the great development of the temporal lobes, which compute invariant representations of faces, which make this functionality in the orbitofrontal cortex possible (Rolls 2012a, 2016a).

This system has also been shown to be present in humans. For example, Kringelbach and Rolls (2003) showed that activation of a part of the human orbitofrontal cortex occurs during a face discrimination reversal task. In the task, the faces of two different individuals are shown, and when the correct face is selected, the expression turns into a smile. (The expression turns to angry if the wrong face is selected.) After a period of correct performance, the contingencies reverse, and the other face must be selected to obtain a smile expression as a reinforcer. It was found that activation of a part of the orbitofrontal cortex occurred specifically in relation to the reversal, that is, when a formerly correct face was chosen, but an angry face expression was obtained. In a control task, it was shown that the activations were not related just to showing an angry face expression. Thus 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 (Kringelbach and Rolls 2003) and occurs when the error neurons in the orbitofrontal cortex become active (Thorpe et al. 1983).

Value is not represented at earlier stages of processing than the orbitofrontal cortex in primates including humans.

Rolls, Scott, and colleagues have shown that the primary taste cortex in the primate anterior insula and adjoining frontal operculum contains not only taste neurons tuned to sweet, salt, bitter, sour (Scott et al. 1986a; Yaxley et al. 1990; Rolls and Scott 2003; Scott and Plata-Salaman 1999), and umami as exemplified by monosodium glutamate (Baylis and Rolls 1991; Rolls et al. 1996a) but also other neurons that encode oral somatosensory stimuli including viscosity, fat texture, temperature, and capsaicin (Verhagen et al. 2004). None of the insular taste cortex neurons had responses to olfactory stimuli, and none could be shown to have responses to visual stimuli that were clearly not just related to mouth movements and the accompanying somatosensory input (Verhagen et al. 2004), in contrast to the orbitofrontal cortex where responses to olfactory and visual stimuli associated with food are common (Thorpe et al. 1983; Rolls et al. 1996b, c, 2010; Critchley and Rolls 1996a, b; Rolls 2015c). Water can activate some neurons in cortical taste areas (Rolls et al. 1990; Yaxley et al. 1990), and this has also been found in the rodent insula (MacDonald et al. 2012). Whether this is by mouth feel relative to saliva, or by ionic content relative to saliva, or by some other mechanism, is not known.

Neurons in the macaque primary taste cortex do not represent the reward value of taste, that is, the appetite for a food, in that their firing is not decreased to zero by feeding the taste to satiety (Yaxley et al. 1988; Rolls et al. 1988). This was confirmed in 17 separate experiments on neurons in the insular and frontal opercular primary taste cortex, using anatomical confirmation that these neurons were in the primary taste cortex by the use of X-ray localization and then histological reconstruction. The neurons showed no reduction in their firing to the taste (typically glucose) after it had been fed to satiety (Yaxley et al. 1988; Rolls et al. 1988).

In macaques, neural processing peripheral to the primary taste cortex is consistent with this, with taste responses found in the rostral part of the nucleus of the solitary tract (Scott et al. 1986b) that are not influenced by feeding to satiety (Yaxley et al. 1985).

Consistently, in humans, BOLD activations in the insular taste cortical area were linearly related to the intensity but not the pleasantness of the tastes (Grabenhorst and Rolls 2008). The converse was found for the orbitofrontal cortex: the BOLD activations in the orbitofrontal cortex but not the anterior and mid-insular taste cortical areas were linearly related to the pleasantness of the tastes (Grabenhorst and Rolls 2008).

For odour, there are similar findings, with activations in the pyriform cortex correlated with the intensity of odours and not their pleasantness, whereas in the orbitofrontal cortex activations are correlated with the pleasantness of odours, but not with their intensity (Rolls et al. 2003).

Consistently, for visual stimuli, the reward value of objects including the sight of food are not represented in the inferior temporal visual cortex in that there is no effect of feeding to satiety, and reversal of reward value does not reverse neuronal responses in the inferior temporal visual cortex (Rolls et al. 1977).

In rodents, reward value is represented even in the first taste relay in the brain, and in the olfactory bulb; and there are direct subcortical pathways.

First, there are major anatomical differences in the neural processing of taste in rodents and primates (Rolls and Scott 2003; Small and Scott 2009; Scott and Small 2009; Rolls 2014, 2015c). In primates, the rostral part of the nucleus of the solitary tract (NTS, the first central taste relay) projects to the taste thalamus and thus to the cortex (Figs. 12.1 and 12.4); whereas in rodents the majority of NTS taste neurons project to the pontine parabrachial nucleus (PbN), referred to as the rodent 'pontine taste area' (Small and Scott 2009; Cho et al. 2002) (Fig. 12.4). From the PbN, the rodent gustatory pathway bifurcates into two pathways: (1) a ventral 'affective' projection to the hypothalamus, central grey, ventral striatum, bed nucleus of the stria terminalis, and amygdala; and (2) a dorsal 'sensory' pathway, which first synapses in the thalamus and then the agranular and dysgranular insular gustatory cortex (Norgren and Leonard 1971; Norgren 1974, 1976, 1990) (Fig. 12.4). In primates (including humans) there is strong evidence to indicate that the PbN gustatory relay is absent (Small and Scott 2009).

Second, a functional difference of rodent taste processing from that of primates is that physical and chemical signals of satiety have been shown to reduce the taste responsiveness of neurons in the nucleus in the solitary tract, and the pontine taste

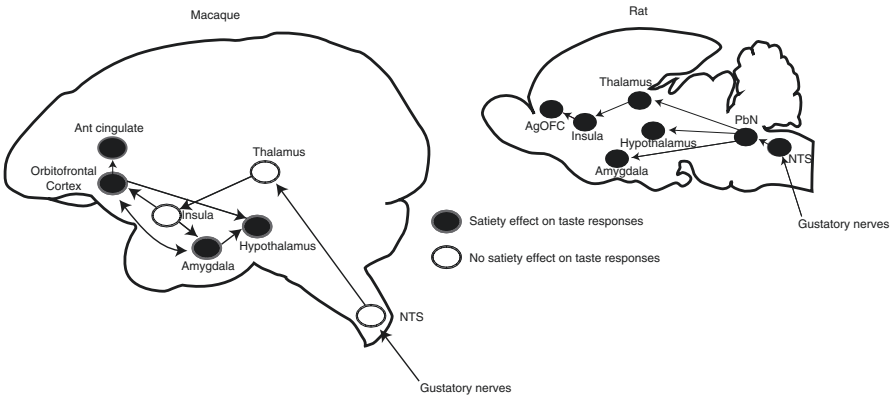

Fig. 12.4 Taste pathways in the macaque and rat. In the *macaque*, gustatory information reaches the nucleus of the solitary tract (NTS), which projects directly to the taste thalamus (ventral posteromedial nucleus, pars parvocellularis, VPMpc) which then projects to the taste cortex in the anterior insula (insula). The insular taste cortex then projects to the orbitofrontal cortex and amygdala. The orbitofrontal cortex projects taste information to the anterior cingulate cortex. Both the orbitofrontal cortex and the amygdala project to the hypothalamus (and to the ventral striatum). In macaques, feeding to normal self-induced satiety does not decrease the responses of taste neurons in the NTS or taste insula (and by inference not VPMpc) (see text). In the *rat*, in contrast, the NTS projects to a pontine taste area, the parabrachial nucleus (PbN). The PbN then has projections directly to a number of subcortical structures, including the hypothalamus, amygdala, and ventral striatum, thus bypassing thalamocortical processing. The PbN in the rat also projects to the taste thalamus (VPMpc), which projects to the rat taste insula. The taste insula in the rat then projects to an agranular orbitofrontal cortex (AgOFC), which probably corresponds to the most posterior part of the primate OFC, which is agranular. (In primates, most of the orbitofrontal cortex is granular cortex, and the rat may have no equivalent to this (Small and Scott 2009; Passingham and Wise 2012; Rolls 2014; Wise 2008; Rolls 2015c.) In the rat, satiety signals such as gastric distension and satiety-related hormones decrease neuronal responses in the NTS (see text), and by inference therefore in the other brain areas with taste-related responses, as indicated in the figure

area, of the rat, with decreases in the order of 30% (Scott and Small 2009; Rolls and Scott 2003; Glenn and Erickson 1976; Giza and Scott 1983, 1987; Giza et al. 1993; Hajnal et al. 1999). (Given this evidence, as expected, neuronal responses in many areas of the rat brain including the insula and amygdala are decreased by satiety (de Araujo et al. 2006).) The implication of this whole body of evidence is that in rodents, sensory (perceptual) and reward (hedonic) processing are not independent. In contrast, in primates, the reward value of tastants is represented in the orbitofrontal cortex in that the responses of orbitofrontal cortex taste neurons are modulated by hunger in just the same way as is the reward value or palatability of a taste, and this is not found in the taste insula (Rolls 2015c). Thus in the primary taste cortex of nonhuman primates (and at earlier stages of taste processing including the nucleus of the solitary tract (Yaxley et al. 1985)), the reward value of taste is not represented, and instead the identity and intensity of the taste are represented (Rolls 2014). A perceptual correlate of this is that when humans feed to satiety, the intensity of the flavour changes very little, whereas the pleasantness of the flavour

decreases to zero (Rolls et al. 1983), showing that in humans perceptual representations of taste and olfaction are kept separate from hedonic representations. This is adaptive, in that we do not go blind to the sight, taste, and smell of food after eating it to satiety and can therefore still learn about where food is located in the environment even when we are not hungry (Rolls 2014). Moreover, and consistently, activations in the human insular primary taste cortex are related to the intensity and not to the pleasantness of taste (Grabenhorst et al. 2008; Grabenhorst and Rolls 2008).

The importance of cortical processing of taste in primates, first for identity and intensity in the primary taste cortex, and then for reward value in the orbitofrontal cortex, is that both types of representation need to be interfaced to visual and other processing that requires cortical computation. For example, it may have adaptive value to be able to represent exactly what taste is present and to link it by learning to the sight and location of the source of the taste, even when hunger is not present and reward is not being produced, so that the source of that taste can be found in future, when it may have reward value. More generally, when we see and taste a food (perhaps in a particular place) when hunger is not present and the food has no reward value, it is still important to be able to learn associations between these representations, including for semantic memory. In line with cortical processing to dominate the processing of taste in primates, there is no modulation in primates of taste responsiveness at or before the primary taste cortex, and the pathways for taste are directly from the nucleus of the solitary tract in the brainstem to the taste thalamus and then to the taste cortex (Figs. 12.1 and 12.4) (Rolls 2014, 2015a).

12.5 Rapid, Rule-Based Reward Reversal Learning in Primates: Orbitofrontal Cortex vs. Amygdala

In primates and humans, the orbitofrontal cortex implements one-trial rule-based reversal learning, and this is important in rapidly updating social behaviour. This is rapid updating of value-based representations.

Visual-to-taste association learning and its reversal by neurons in the orbitofrontal cortex can take place in as little as one trial (Thorpe et al. 1983; Rolls et al. 1996b; Deco and Rolls 2005; Rolls and Deco 2016). This is rule-based, in that if on one trial the expected reward is not obtained, on the very next trial a previously punished visual stimulus is shown, it will be chosen on the basis that the rule for which stimulus is associated with reward has changed. This has clear adaptive value in enabling particular foods with a good or bad taste to be learned and recognized quickly, important in foraging and in food selection for ingestion. The visual inputs reach the orbitofrontal cortex from the inferior temporal visual cortex, where neurons respond to visual objects independently of their reward value (e.g. taste) as shown by satiety and reversal learning tests (Rolls et al. 1977; Rolls 2008b, 2012a). The visual-to-taste associations are thus learned in the orbitofrontal cortex (Rolls 2014). These visual-taste neurons thus respond to expected value (Rolls 2014). Consistent evidence is available in humans, in that the lateral orbitofrontal cortex is

activated on reversal trials, when an error is detected (Kringelbach and Rolls 2003), consistent with the presence of error neurons in the primate orbitofrontal cortex (Thorpe et al. 1983; Rolls 2016a). Further, patients with damage to the orbitofrontal cortex are impaired on rapid stimulus-reward reversal learning (Hornak et al. 2004; Rolls et al. 1994). Maintaining the current rule in short-term memory and using this to bias neurons in the orbitofrontal cortex may be one computation that granular prefrontal cortex facilitates, because of its highly developed local recurrent collateral system which can form an attractor network and hold the current rule in short-term memory (Rolls 2016a; Rolls and Deco 2016). Rodents may not be able to perform one-trial rule-based stimulus-reward reversal.

The amygdala is a structure in the temporal lobe with somewhat similar connections to the orbitofrontal cortex (see Fig. 12.1). The amygdala has been present in evolution for much longer than the primate orbitofrontal cortex and appears to differ from the orbitofrontal cortex in that it cannot implement one-trial, rule-based, visual discrimination reversal when the taste or flavour associated with the visual stimulus is reversed (Rolls 2014). The primate amygdala contains neurons that respond to taste and oral texture (Sanghera et al. 1979; Scott et al. 1993; Kadohisa et al. 2005a, b). Some neurons respond to visual stimuli associated with reinforcers such as taste but do not reflect the reinforcing properties very specifically, do not rapidly learn and reverse visual-to-taste associations, and are much less affected by reward devaluation by feeding to satiety than are orbitofrontal cortex neurons (Sanghera et al. 1979; Yan and Scott 1996; Kadohisa et al. 2005a, b; Wilson and Rolls 2005; Rolls 2014). The primate orbitofrontal cortex appears to be much more closely involved in flexible (rapidly learned, and affected by reward devaluation) reward representations than in the primate amygdala (Rolls 2014), although both amygdala and orbitofrontal cortex lesions can impair the preference for an object on the first trial after devaluation by feeding to satiety of the food-related value of that object (Murray and Izquierdo 2007). In addition, in humans, amygdala lesions appear to have less profound effects on emotion and emotion-related learning than do orbitofrontal cortex lesions (Rolls 2014).

12.6 Neuroeconomic Representation of Value in the Primate Including Human Orbitofrontal Cortex

The reward value representations in the primate orbitofrontal cortex of taste, olfactory, and flavour stimuli are appropriate for economic decision-making in a number of ways (Rolls 2014, 2015c). First, the responses of orbitofrontal cortex neurons reflect the quality of the commodity or 'good' (e.g. the sight or taste of food) multiplied by the amount available (Padoa-Schioppa and Assad 2006; Padoa-Schioppa 2011). In humans, activations in the orbitofrontal cortex reflect the 'subjective value' of foods (where 'subjective value' in economics refers strictly to what is chosen by a subject rather than to conscious subjective pleasantness (Rolls 2014, 2015c)), assessed in a task in which the value is measured by choices between

different foods and different amounts of money (Plassmann et al. 2007). Moreover these neurons reflect the value of reward stimuli, and not actions made to obtain them (Rolls 2014; Thorpe et al. 1983; Rolls et al. 1990; Verhagen et al. 2003; Padoa-Schioppa and Assad 2006).

The value representation in the primate and human orbitofrontal cortex is domain general, in that the amount and value of goods, and temporal discounting, operate transitively (as shown by trade-offs), providing a basis for economic decision-making (Padoa-Schioppa 2011; Rolls 2014). There is evidence that this is not the case in rodents (Padoa-Schioppa 2011; Rolls 2014).

Goal-directed choice may be the best measure of value and emotion, for there are many partly separate neural circuits for different emotion-related responses, e.g. autonomic output, freezing, fixed action patterns, and unconditioned approach or withdrawal. The functions of the amygdala.

Given the approach to emotions as states elicited by instrumental reinforcers, goal-directed value as a basis for action is a crucial system in emotion (Rolls 2014). However, some of the brain structures implicated in emotion produce other outputs that are adaptive, even if not fundamental to emotion and goal-directed behaviour [section 4.6.1 (pp. 159–165) of Emotion and Decision-Making Explained (Rolls 2014), and Cardinal et al. (2002)], though possibly of earlier evolutionary origin.

First, autonomic responses such as increased heart rate can be produced by brainstem pathways, the hypothalamus, amygdala, orbitofrontal cortex, and cingulate cortex (Figs. 12.1 and 12.2) (Critchley and Harrison 2013). Autonomic responses can become classically conditioned in structures such as the amygdala, as can freezing responses (LeDoux 2012; Phelps and LeDoux 2005), but of course these are conditioned reflexes, with no flexibility of response (Rolls 2014). Even approach to a food can become classically conditioned (Cardinal et al. 2002; Rolls 2014).

Second, the striatum/basal ganglia route, evolutionarily old, which receives from the amygdala as well as the cortex, is involved in learning stimulus-response habits, which tend to be overlearned and are not under the direct control of the goal value (Figs. 12.1 and 12.2) (Rolls 2014).

In this context, it is interesting to consider the role of the amygdala in these types of response and in emotion. Neurons in the primate amygdala do not show rapid, one-trial reversal nor are their responses very consistently reduced to zero by devaluation produced, for example, by feeding to satiety (Sanghera et al. 1979; Rolls and Scott 2003; Rolls 2014). This is in contrast to the orbitofrontal cortex (Rolls 2014), though amygdala neurons may be more involved when aversive stimuli are used (Morrison et al. 2011). Lesions of the macaque amygdala do not impair stimulus-reward reversal learning, whereas lesions of the orbitofrontal cortex do (Murray and Izquierdo 2007). Lesions of the rodent amygdala impair many classically conditioned responses such as autonomic responses and freezing (LeDoux 2012; Phelps and LeDoux 2005; Cardinal et al. 2002; Rolls 2014), and the importance of the rat amygdala, with its much less well-developed orbitofrontal cortex than primates, in

olfactory reversal learning, has been emphasized (Schoenbaum et al. 1999). Further, the changes in emotion in patients with amygdala lesions are much less marked than those in patients with orbitofrontal cortex damage, and special tests, analogous in some cases to those developed in rodent studies, are necessary to reveal deficits (Phelps and LeDoux 2005; Whalen and Phelps 2009). For example, patients with amygdala lesions are impaired at learning classically conditioned skin conductance responses when a blue square is associated with a shock and are also impaired in acquiring the same autonomic response to fear by verbally instructed learning or by observational learning. The human amygdala appears to be important mainly for some fear responses to some stimuli, such as whether an individual backs off in a social encounter (Feinstein et al. 2011).

Taken together, these findings provide evidence that in primates including humans the amygdala becomes overshadowed by the orbitofrontal cortex. The orbitofrontal cortex has a much more important role in the computation of reward and punishment value, as measured by effects of devaluation and goal-directed one-trial rule-based learning and reversal, and thereby in emotion, which shows major changes after damage to the orbitofrontal cortex (Hornak et al. 1996, 2003, 2004,; Rolls et al. 1994; Rolls 2014). The computational bases are considered elsewhere of primate one-trial rule-based reversal (Deco and Rolls 2005), how non-reward neuronal activity is computed in the orbitofrontal cortex (Rolls and Deco 2016), and how these process may be related to depression considered as involving emotions produced by non-reward (Rolls et al. 2016; Rolls 2016c). The computational bases for the importance of the orbitofrontal cortex in emotion are described in *Cerebral Cortex: Principles of Operation* (Rolls 2016a), which also considers more widely the ways in which the cerebral cortex has evolved.

Goal value-directed choice is usual in primates and humans, whereas fixed action patterns, such as pecking in birds, are more common elsewhere.

The computation of reward value, and then its use as the target for goal-directed learning under the control of the goal value, is a flexible way for genes to influence behaviour and appears to be at the heart of primate including human emotion. However, genes may also encode stimulus-response reflexes, and this is seen, for example, in the pecking of birds at grain-like objects (Rolls 2014; Brown and Jenkins 1968).

In humans, and perhaps some primates, syntactic reasoning and thereby planning allow selfish gene-specified (emotion-related) rewards to be rejected in favour of the long-term interests of the individual, the phenotype.

The evolutionary adaptive value of emotions is that different genes specify different goals in their own self-interest, and actions can then be learned and performed by instrumental learning to obtain the goals. In addition, a rational thought system involved in multistep planning using syntax can allow gene-specified goals to be deferred or avoided in order to achieve longer-term types of goal that may be more advantageous to the individual than to the genes (Rolls 2012b, 2014). Decisions between these systems are likely to be taken by a probabilistic cortical attractor decision-making network (Rolls and Deco 2010; Rolls 2014).

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