



Discussion forum

Emotion and decision-making explained: A précis



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1. Introduction

Emotion and Decision-Making Explained aims to explain and advance understanding of emotion and decision-making at two levels of explanation. One is the *proximate*, mechanistic level of explanation, in terms of brain mechanisms. In terms of decision-making, this results in emphasis on biologically plausible integrate-and-fire models of the attractor neuronal network processes that underlie decision-making, rather than the phenomenological models such as the drift-diffusion model, although these phenomenological models of decision-making are covered in Appendix B. The second is the *ultimate* level of explanation, the level of adaptive value in evolution, in which emotion is explained as an efficient and simple way for genes to influence behaviour for their own 'selfish' reproductive success, by specifying the rewarding and punishing goals for instrumental actions, with the resulting states when the rewards or punishers are or are not obtained being emotional states (Chapters 2 and 3). This is simpler and more efficient in terms of evolutionary adaptive value than for genes to specify the details of the actions, the behavioural responses, to be produced by stimuli.

A further aim of *Emotion and Decision-Making Explained* is to produce a unifying approach to emotion and neuroeconomics, which are both concerned with the valuation of rewards and punishers, and to link these valuation processes to how decisions are then made based on the valuations.

Emotions are defined in this book as states elicited by rewards and punishers, that is, by instrumental reinforcers, which are the goals for action. The concept is that almost any action can be performed to obtain the goal. A goal might be for example obtaining the taste of a delicious food or a

pleasant touch. The goal must be motivating, must when obtained elicit emotional states which are rewarding and reinforce the action just made, and the goal must exist to direct behaviour independently of pre-specified responses or habits. Thus the motivational states must exist and often continue for considerable periods until an action is performed that obtains the goal; and the emotional state may continue for long periods when the goal is obtained, and especially when the goal is not obtained, in order to direct further action. The emotional and motivational states may be contrasted with responses or reflexes which can occur unconditionally to stimuli (for example autonomic responses to stimuli that prepare the body for activity, and reflexes such as freezing or flight), for which no intervening state of motivation or emotion is required, as they are reflexes, which can become classically conditioned. These issues of the nature of emotion, and its functions, are covered in Chapters 2 and 3.

The topics covered in *Emotion and Decision-Making Explained* include in addition the following (see http://www.oxcns.org/b11_text.html):

The brain mechanisms underlying emotion. This Chapter includes the orbitofrontal cortex (OFC), amygdala, the anterior cingulate cortex involved in emotion but not the posterior cingulate cortex involved in spatial function and memory (Rolls, 2014b), and the insula.

Food reward value, pleasure, and appetite.

The pharmacology of emotion, reward, and addiction, including the functioning of the basal ganglia and the functions of dopamine.

Sexual behaviour, reward, and brain function; sexual selection of behaviour. This includes the bases for attraction

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between males and females, and an ‘ultimate’ explanation for the reward value of sex.

Decision-making mechanisms (This includes the advantages of the probabilistic decision-making performed by spiking attractor neuronal networks in the brain.).

Neuroeconomics and decision-making.

Emotional feeling and consciousness: a theory of consciousness, and the basis for subjective feelings of pleasure.

The selection of behaviour by the emotional, goal-related, system; by the habit and stimulus–response systems; and by the explicit, reasoning system.

Links between emotion, ethics, and aesthetics.

Neural networks and emotion-related learning, including pattern association neuronal networks, autoassociation neuronal networks, and reinforcement learning.

Decision-making models, including the phenomenological models of decision-making including drift-diffusion and race models; and a formal description of the integrate-and-fire attractor network model of decision-making.

The book is intended for all interested in emotion and decision-making, including those from the undergraduate level upwards from the areas of neuroscience, neurology, psychology, psychiatry, biology, animal behaviour, economics, and philosophy.

2. Some conclusions reached in Emotion and Decision-Making Explained

To provide a view of where the book leads, I summarize some of the points made and conclusions reached in the book, with the details of the evidence provided in the book from neuroanatomy, neuronal recordings, the effects of brain lesions, functional neuroimaging, and computational neuroscience.

1. A scientific approach to emotion, its nature, and its functions, is provided (Chapters 2 and 3). This approach, based on many different rewards and punishers, and based on the reinforcement contingencies that apply for each of very many different rewards and punishers, provides a foundation for classifying different emotions (Chapter 2), for understanding what information processing systems in the brain are involved in emotion, and how each brain system is involved in emotion (Chapters 4–6).

2. A quite specific view is reached about how brains are designed around reward and punishment value systems, because this is the way that genes can build a complex system that will produce appropriate but flexible behaviour to increase their fitness (Chapter 3). The way that evolution by natural selection does this is to build us with reward and punishment systems that will direct our behaviour towards goals in such a way that survival and in particular reproductive fitness are achieved. By specifying goals, rather than particular responses, genes leave much more open the possible behavioural strategies that might be required to increase their fitness. Specifying particular responses would be inefficient in terms of behavioural flexibility as environments change during evolution, and also would be more genetically costly to specify (in terms of the information to be encoded

and the possibility of error). This view of the evolutionary adaptive value for genes to build organisms using reward- and punishment-decoding and action systems in the brain places one squarely in line as a scientist developing ideas from Darwin (1859) onwards (Dawkins, 1976; Hamilton, 1964, 1996), and is a key part of Rolls’ theory of emotion.

The theory helps in understanding much of sensory information processing in the brain, followed by reward and punishment value encoding, followed by decision-making and action selection to obtain the goals identified by the sensory/reinforcer decoding systems. Value coding systems must be separate from purely sensory or motor systems, and while a goal is being sought, or if a goal is not obtained, the value-related representation must remain to direct further goal-directed behaviour, and it is these continuing goal-related states to which emotion is related.

3. The importance of reward and punishment systems in brain design helps us to understand not only the significance and importance of emotion, but also of motivational behaviour, which frequently involves working to obtain goals that are specified by the current state of internal signals to achieve homeostasis (Chapter 5 on hunger) or are influenced by internal hormonal signals (Chapter 7 on sexual behaviour). Indeed, motivation may be seen as a state in which one is working for a goal, and emotion as a state that occurs when the goal, an instrumental reinforcer, is obtained or is not obtained, and that may persist afterwards. The concept of gene-defined reinforcers providing the goals for action helps in understanding the relation between motivational states (or desires) and emotion, as the organism must be built to be motivated to obtain the goals, and to be placed in a different state (emotion) when the goal is or is not achieved by the action. Emotional states may be motivating, as in frustrative non-reward. The close but clear relation between motivation and emotion is that both involve what humans describe as affective states (e.g., feeling hungry, liking the taste of a food, feeling happy because of a social reinforcer), and both are about goals.

4. I outline in Chapters 4–6 what may be the fundamental architectural and design principles of the brain for sensory, reward value, and punishment value information processing in primates including humans. These architectural principles include the following (see Fig. 1):

- (a) For potential secondary reinforcers, analysis is to the stage of invariant object identification (in for example the inferior temporal visual cortex) before reward and punisher associations are learned at a later stage of processing. The reason for this is to enable correct perceptual generalization to other instances of the same or similar objects, even when a reward or punisher has been associated with one instance previously.
- (b) The representation of the object is (appropriately) in a form that is ideal as an input to pattern associators that allow the reinforcement associations to be learned. The representations are appropriately encoded in that they can be decoded by dot product decoding of the type that is very neurally plausible; are distributed so allowing excellent generalization and graceful degradation; have relatively independent information conveyed by

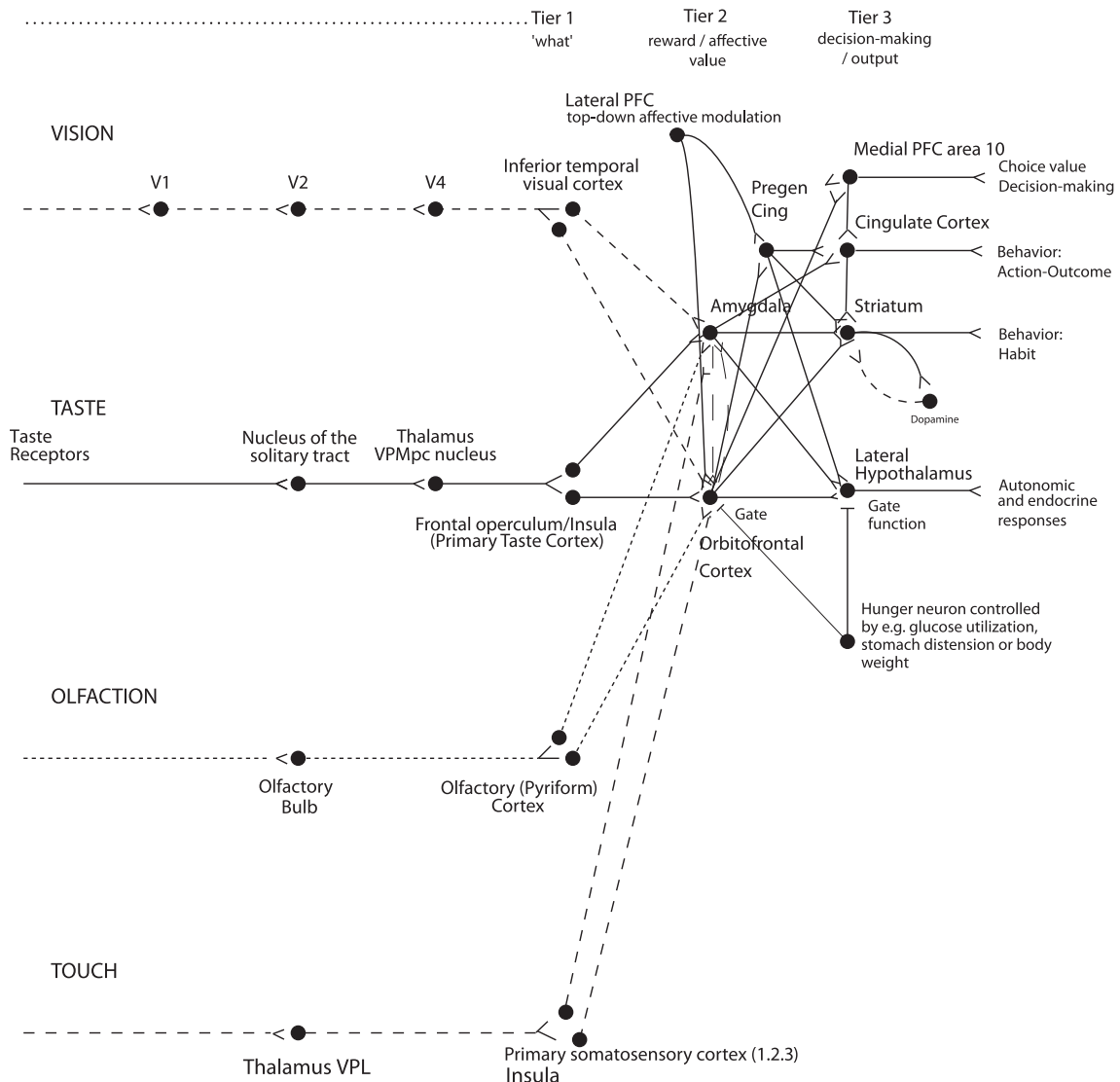


Fig. 1 – Schematic diagram showing some of the connections of the taste, olfactory, somatosensory, and visual pathways in the brain. V1, primary visual (striate) cortex; V2 and V4, further cortical visual areas. PFC, prefrontal cortex. VPL, ventro-postero-lateral nucleus of the thalamus, which conveys somatosensory information to the primary somatosensory cortex (areas 1, 2 and 3). VPMpc, ventro-postero-medial nucleus pars parvocellularis of the thalamus, which conveys taste information to the primary taste cortex. Pregen Cing, pregenual cingulate cortex. For purposes of description, the stages can be described as Tier 1, representing what object is present independently of reward value; Tier 2 in which reward value is represented; and Tier 3 in which decisions between stimuli of different value are taken, and in which value is interfaced to behavioural output systems.

different neurons in the ensemble thus allowing very high capacity; and allow much of the information to be read off very quickly, in periods of 20–50 msec [see Chapter 4 on the brain mechanisms of emotion, Appendix A on neural networks, Rolls (2008), and Rolls and Treves (2011)].

- (c) An aim of processing in the ventral visual system (which projects to the inferior temporal visual cortex) is to help select the goals, or objects with reward or punisher associations, for actions. Action is concerned with the identification and selection of goals, the targets for action. The ventral visual system is crucially involved in

this. I thus extend the concept of Milner and Goodale (1995) that the dorsal visual system is for actions, and the ventral visual system for ‘perception’, e.g., perceptual and cognitive representations. I argue that the ventral visual system is concerned with selecting the goals for action. It does this by providing invariant representations of objects, with a representation that is appropriate for interfacing to systems (such as the amygdala and OFC, see Chapter 4, and Figs. 4.2, 4.3, and 10.4) which determine using pattern association the reward or punishment value of the object, as part of the process of selecting which goal is appropriate for action.

Some of the evidence for this described in Chapter 4 is that large lesions of the temporal lobes (which damage the ventral visual system and some of its outputs such as the amygdala) produce the Kluver–Bucy syndrome, in which monkeys select objects indiscriminately, independently of their reward value, and place them in their mouths. The dorsal visual system helps with executing those actions, for example with shaping the hand appropriately to pick up a selected object. (Often this type of sensori-motor operation is performed implicitly, i.e., without conscious awareness.) In so far as explicit planning about future goals and actions requires knowledge of objects and their reward or punisher associations, it is the ventral visual system that provides the appropriate input for planning future actions. Further, for the same reason, I propose that when explicit, or conscious, planning is required, activity in the ventral visual system will be closely related to consciousness, because it is to objects, represented in the ventral visual system, that we normally apply multistep planning processes (as described in Chapter 10).

- (d) For primary reinforcers, the reward decoding may occur after several stages of processing, as in the primate taste system in which reward is decoded only after the primary taste cortex. The architectural principle here is that in primates there is one main taste information-processing stream in the brain, via the thalamus to the primary taste cortex, and the information about the identity of the taste is not biased by modulation of how good the taste is before the insular primary taste cortex, so that the taste representation in the primary taste cortex can be used for purposes that are not reward-dependent. One example might be learning where a particular taste can be found in the environment, even when the primate is not hungry and therefore the taste is not currently rewarding. For this, the primary taste cortex provides a representation of what the taste is independently of its reward value (Grabenhorst & Rolls, 2008; Yaxley, Rolls, & Sienkiewicz, 1988).

In the case of some sensory systems, the reinforcement value may be made explicit early on in sensory processing. This occurs, for example, in the pain system. The architectural basis of this is that there are different channels (nerve fibres) for pain and touch, so that the affective value and the identity of a tactile stimulus can be carried by separate parallel information channels, allowing separate representation and processing of each. In contrast, for vision, invariant visual object recognition must be performed before reward can be assigned to an object, and that underlies much cortical architecture, with object identification occurring before reward decoding.

- (e) In non-primates including, for example, rodents, the design principles may involve less sophisticated design features, partly because the stimuli being processed are simpler. For example, view-invariant object recognition is probably much less developed in non-primates, with the recognition that is possible being based more on physical similarity in terms of texture, colour, simple features, etc., rather than in terms of shape that

involves the combination of many features in a particular spatial relationship (Rolls, 2008; Rolls & Deco, 2002). It may be because there is less sophisticated cortical processing of visual stimuli in this way that other sensory systems are also organized more simply in rodents, with, for example, some (but not total, only perhaps 30%) modulation of taste processing by hunger early in sensory processing in rodents (Rolls & Scott, 2003; Scott, Yan, & Rolls, 1995). Further, while it is appropriate usually to have emotional responses to well-processed objects (e.g., the sight of a particular person), there are instances, such as a loud noise or a pure tone associated with punishment, where it may be possible to tap off a sensory representation early in sensory information processing that can be used to produce emotional responses, and this may occur, for example, in rodents, where the subcortical auditory system provides afferents to the amygdala (see Chapter 4). For these reasons, emphasis is placed in the book on research in primates including humans.

- (f) Another design principle is that the outputs of the reward and punishment value systems must be treated by the action system as being the goals for action. The action systems must be built to try to maximize the activation of the representations produced by rewarding events, and to minimize the activation of the representations produced by punishers or stimuli associated with punishers. Drug addiction produced by the psychomotor stimulants such as amphetamine and cocaine can be seen as activating the brain at the stage where the outputs of the amygdala and OFC, which provide representations of whether stimuli are associated with rewards or punishers, are fed into the ventral striatum to influence approach behaviour. The fact that addiction is persistent may be related to the fact that because the outputs of the amygdala and OFC are after the stage of stimulus–reinforcer learning, and after sensory-specific satiety has been computed, the action system has to be built to interpret the representations the amygdala and OFC provide as meaning reward value, and a goal for action.

5. Especially in primates, the visual processing for emotional and social behaviour requires sophisticated representation of individuals, and for this there are many neurons devoted to face processing (Rolls, 2011). In addition, there is a separate system that encodes face gesture, movement, and view, as all are important in social behaviour, for interpreting whether a particular individual, with his or her own reinforcement associations, is producing threats or appeasements (Rolls, 2011, 2012b).

6. After mainly unimodal processing to the object level, sensory systems then project into convergence zones. Those especially important for reward and punishment, emotion and motivation, are the OFC and amygdala (see Fig. 1), where primary reinforcers are represented to encode *outcome value*. These parts of the brain appear to be especially important in emotion and motivation not only because they are the parts of the brain where in primates the primary (unlearned) reinforcing value of stimuli is represented, but also because they

are the parts of the brain that perform pattern-association learning between potential secondary reinforcers and primary reinforcers to compute *expected value*. They are thus the parts of the brain involved in learning the emotional and motivational reward value of many stimuli.

The OFC is involved in the rapid, one-trial, reversal of emotional behaviour when the reinforcement contingencies change, and this may be implemented by switching a rule, as described in Section 4.5.7. These OFC neurons may be described as *expected value neurons*. This rapid, rule-based, reversal and re-valuation of stimuli to encode their current reward value in one-trial and using rules may be a computation made possible by the development of the granular OFC and connected areas that are not present in rodents (Section 1.3). The *negative reward prediction error neurons* [which respond when an expected reward is not obtained (Thorpe, Rolls, & Maddison, 1983)] found in the OFC are thought to be involved in the rule-based reward reversal implemented in the OFC.

7. The different reward valuation systems are specified to have values scaled appropriately by genes to lead to their selection in such a way that reproductive success is maximized. In addition, the reward systems are specific, encode the value of specific rewards and punishers, and have tendencies to self-regulate, so that they operate on a common value scale that leads to the selection of different rewards with appropriately balanced probabilities, and often depending on modulation by internal motivational signals. The presence of many different specific reward value systems operating with a *common scale of value* helps each reward to be selected to maximize reproductive success. There is *no conversion* to a *common currency*, as this would no longer encode the specific reward to which the action system should direct action. The value of a reward or punisher specified by genes may be rescaled by learning, as in taste aversion learning and conditioned appetite and satiety.

8. A principle that assists the selection of different behaviours is sensory-specific satiety, which builds up when a reward is repeated for a number of minutes, and is implemented in the OFC (Critchley & Rolls, 1996; Krangelbach, O'Doherty, Rolls, & Andrews, 2003; Rolls, Sienkiewicz, & Yaxley, 1989). A principle that helps behaviour to lock on to one goal for at least a useful period is incentive motivation, the process by which early on in the presentation of a reward there is reward potentiation. There are probably simple neurophysiological bases for these time-dependent processes in the reward (as opposed to the early sensory) systems that involve synaptic habituation and (non-associative) facilitation respectively.

9. With the advances made in the last 30 years in understanding the brain mechanisms involved in reward and punishment, and emotion and motivation, the basis for addiction to drugs is becoming clearer, with dopamine playing an important role, particularly in the conditioned reinforcing effects of stimuli associated with drug usage, which influence 'wanting' for the addictive substance. Further, now that we are starting to understand how different brain systems contribute to emotion, this provides a better foundation for developing pharmacological and deep brain stimulation treatments for depression and anxiety that may target particular brain areas (Chapter 6).

10. The representation in the OFC appears indeed to represent economic value, in that neuronal responses and neural activations appear to be related closely to what is chosen, and also to the conscious subjective value or pleasantness rating placed on a 'good'. The OFC activity reflects by these measures of *economic value* the effects of risk (the probability that a reward will be available), of ambiguity (whether the outcome probability is known), of temporal discounting, and of the trade-off between the amount of the good that is available and the value of the good (Glimcher & Fehr, 2013; Padoa-Schioppa, 2011). Value is represented on a continuous scale in the OFC, and indeed OFC activations are linearly related to the subjective pleasantness (medially) or unpleasantness (laterally) of stimuli or events (Grabenhorst & Rolls, 2008; Rolls, Krangelbach, & de Araujo, 2003).

11. The reward value placed on different rewards and the punishment value placed on different non-rewards or punishers will be different between different individuals, as a result of genetic variation for natural selection. Also, most humans cannot perform economic calculations of the expected value of different choices, as the human brain operates primarily by similarity comparisons and not by logical calculations of the type implemented in digital computers (Rolls, 2008, 2012c). For these reasons, classical microeconomics with its approach of a few axioms and a rational actor can no longer be considered as what really may account for the behaviour of humans and other animals. Instead, classical (micro)economics [see Glimcher (2011)] may be replaced by an understanding in neuroeconomics of how heuristics guided by evolution make different rewards and costs become differently scaled in different individuals, and further how choices may be selected by a decision-making process based on in-built and probabilistic heuristics rather than by correctly computed calculations in a rational, reasoning, decision-making actor.

12. The OFC represents the value of stimuli. Its neurons respond to stimulus value, and not to behavioural responses. The OFC provides outputs to:

- (a) the anterior cingulate cortex for goal-directed actions taking into account the costs of the actions (Sections 4.6.1.2 and 4.7), and for which positive value is represented in the pregenual anterior cingulate cortex and negative value more dorsally, for interfacing to motor/action representations in the mid-cingulate cortex (Grabenhorst & Rolls, 2011);
- (b) the basal ganglia for stimulus–response habits (Sections 4.6.1.2, 6.3 and 6.8);
- (c) with the amygdala implements Pavlovian learning processes that enable stimuli to elicit approach or withdrawal as well as affective states that may become the goals for instrumental actions;
- (d) with the amygdala implements Pavlovian learning processes that enable autonomic and endocrine responses to be elicited by conditioned stimuli (Section 4.6.1.1).

13. Decision-making is now understood as a non-linear competition between different attractor states in a spiking attractor neuronal network that results in a single winning

neuronal population. The decision variables bias the neurons in the different possible attractor states. The mechanism is understood at the level of integrate-and-fire neurons with biophysically realistic parameters (Deco, Rolls, Albantakis, & Romo, 2013; Rolls & Deco, 2010; Wang, 2002). The decision-making is probabilistic because of statistical fluctuations introduced by the approximately Poisson nature of the timing of the spikes of the neurons for a given mean firing rate (Chapter 8 and Appendix B).

This understanding is replacing the phenomenological drift-diffusion mathematical models of decision-making with fitted parameters (Appendix B), not only because the attractor neuronal network model is more neurobiologically realistic, but also because it allows the exploration of how biological parameters such as ion channel conductances and the effects of different transmitters expressed through different ion channels influence the operation and stability of the decision-making system. This is enabling medically relevant implications to be investigated, for example to neuropsychiatric disorders including schizophrenia and obsessive-compulsive disorder (Sections 8.11.12 and 8.11.13) (Rolls, 2012a).

14. The spiking neuronal attractor network approach to decision-making is a unifying approach, for the same mechanism applies not only to decision-making, but also to the operation of short-term memory systems, to the recall of information from long-term memory systems, and to top-down attention (Rolls, 2008). Part of the basis for this is that attractor states are a natural property of cortical systems, which are characterized by excitatory local recurrent collateral connections between the pyramidal cells which implement positive feedback; associative synaptic plasticity of these connections; and inhibition between the neurons implemented by GABA neurons (Rolls, 2008).

15. The probabilistic operation of the decision-making process caused by the spiking-related statistical fluctuations in finite-sized attractor neuronal networks has many advantages, including different decisions and memory recall on different occasions even with similar inputs, giving rise to non-deterministic behaviour of the system. This probabilistic behaviour has a useful impact in many situations, including sometimes choosing less favourable options to update knowledge, predator avoidance, social interactions, and creativity (Section 8.11) (Rolls & Deco, 2010). The probabilistic behaviour of the mechanism also makes the brain non-deterministic, and there are implications for free-will (Sections 10.4–10.5) (Rolls, 2012c).

16. These non-linear decision-making attractor neuronal networks that result not only in ‘decisions’ but also in categorization are found in many parts of the cortex, typically after earlier stages of more linear processing that performs analysis of the stimulus. There is not therefore just one decision-maker in the brain, but multiple decision processes for different types of decision, implemented locally in different cortical areas. One type of decision for example is the direction of global optic flow made in the dorsal visual system. In the context of value and hence emotion systems, there is evidence that the more anterior, ventromedial parts of the prefrontal cortex (vmPFC), including medial PFC area 10, are involved in the decision-making between stimuli of different value, and follow in the hierarchy the more linear

representations of specific reward values in the OFC (Chapter 8) (Grabenhorst & Rolls, 2011; Rolls & Grabenhorst, 2008).

17. With respect to the dopamine system, it appears that the activity of the dopamine neurons does not represent reward, and is not correlated with hedonic or emotional states (Chapter 6). Part of the evidence for this is that the dopamine neurons may fire in relation to a reward prediction error, rather than in relation to reward itself (Schultz, 2013), and that damage to the dopaminergic system does not impair hedonic responses or ‘liking’. Dopamine pathways do influence systems involved in Pavlovian (classically conditioned) incentive salience effects mediated by the ventral striatum, and may thereby influence ‘wanting’. However, there are inconsistencies with the dopamine reward prediction error hypothesis, with respect for example to whether the dopamine system is implicated in salience [as many dopamine neurons respond to aversive, novel, and/or alerting stimuli (Bromberg-Martin, Matsumoto, & Hikosaka, 2010)] versus reward error prediction; and whether a positive reward prediction error signal could facilitate the learning of stimuli associated with punishment and the inhibition of actions (Chapter 8).

18 In addition to the implicit system for action selection, in humans and perhaps related animals there is also an explicit system that can use language to compute actions to obtain deferred rewards using a one-off plan. The language system enables one-off multistep plans that require the syntactic organization of symbols to be formulated in order to obtain rewards and avoid punishers. There are thus two separate systems for producing actions to rewarding and punishing stimuli in humans and potentially in related animals. These systems may weight different courses of action differently, and produce conflict in decision-making, in that each can produce behaviour for different goals (immediate vs long-term goals involving multiple step planning). Understanding our evolutionary history is useful in enabling us to understand our emotional decision-making processes, and the conflicts that may be inherent in how they operate (Chapter 10).

19. It is argued that the decisions taken by the emotional system are in the interests of selfish genes, in which the value systems have their foundations. The reasoning, rational, system enables longer-term decisions to be taken by planning ahead, and for the decisions to be in the interests of the individual, the phenotype, instead of the genes. This is another important sense (additional to the sense that genes and environment usually make joint contributions) in which the behaviour of humans and other animals with reasoning systems can be said to be not determined by our genes (Chapter 10).

This rational, reasoning, ‘explicit’ decision-making system provides a basis for the operation of societies in which social contracts underpinned by reasoned understanding provide a basis for stability, and for gene-specified emotional value systems not to provide the only goal [Chapter 10 and Rolls (2012c)]. Understanding the emotional system is very important, for it has major influences on behaviour, and helps us to understand not only individual differences and personality, but also influences on behaviour that may have their origins partly in the different interests (on average) of males and females (Chapter 7). Understanding the emotional and the

rational systems, and their very different types of computation, has many implications for understanding processes as far ranging as aesthetics, economics, ethics, politics, and religion [Chapter 10 and [Rolls \(2012c\)](#)].

20. **Pleasure** is a subjective state reported in humans that is associated with a reward. Just as reward is specific, with many different types of reward, so is pleasure. It is possible that emotional feelings (including pleasure), part of the much larger problem of consciousness, arise as part of a process that involves thoughts about thoughts, which have the adaptive value of helping to correct one-off multistep plans. This is the higher-order syntactic thought (HOST) approach to consciousness described in Chapter 10, but there seems to be no clear way to choose which theory of consciousness is moving in the right direction, and caution must be exercised here, and current theories should not be taken to have implications.

21. Functional neuroimaging and neuropsychological data in humans (Chapters 4–6) are consistent with many of the conclusions based on primate data including neurophysiology which provide the fundamental evidence needed to make computational models of how the brain functions as an information processing system exchanging information between its computing elements, the neurons [see Appendices A and B and [Rolls \(2008\)](#)]. In addition, the human findings provide interesting new evidence on how top–down cognitive and attentional effects can influence emotions in areas such as the orbitofrontal and anterior cingulate cortex (Section 4.5.5.7) ([de Araujo, Rolls, Velazco, Margot, & Cayeux, 2005](#); [Grabenhorst & Rolls, 2008](#); [Grabenhorst, Rolls, & Bilderbeck, 2008](#); [Rolls, Grabenhorst, Margot, da Silva, & Velazco, 2008](#)). The mechanisms by which cognitive states have top–down effects on emotion are probably similar to the biased competition mechanisms that subserve top–down attentional effects ([Deco & Rolls, 2005](#); [Desimone & Duncan, 1995](#); [Rolls, 2008](#); [Rolls & Deco, 2002](#)), though whole linked processing streams of cortical processing may be influenced in a top–down biased activation process by attention to affective value [Section 4.12 and [Rolls \(2013a\)](#)].

22. In relation to animal welfare, the suggestion arises that in addition to being guided by health, it may be useful to be guided by how the animals set their priorities for different rewards and punishers. This follows from the hypothesis that the brain is designed around reward/punisher evaluation systems, and behaviour optimizes obtaining the goals defined by the genes. The degree to which different genes make different reinforcers important, and how the reinforcers are modulated by for example motivational state, then directly influence the value the animal places on a provision. The value or choice of the reinforcer thus provides a useful measure of its ‘importance to the animal’. When making these measures of the value of different instrumental reinforcers, it is important to be aware of the many factors that can influence the selection of a reinforcer. Examples are the fact that if the reinforcer is of low value (for example when tested under zero drive conditions), the choice of the reinforcer is very sensitive to incentive motivational effects, to priming, and to delay of reinforcement; and shows rapid extinction (Chapter 7 of [Rolls \(2005\)](#)). We may also note that the reinforcer value systems in the brain are generally

different to the systems involved in autonomic and endocrine responses (Chapter 4). The implication is that the systems (for reinforcer value vs autonomic/endocrine responses) have evolved separately, and that the autonomic/endocrine responses elicited in emotion-provoking situations may not necessarily be a good guide to the instrumental reinforcing value (as measured by choice) or ‘importance’ of the resource to the animal.

23. The processes and systems involved in emotion have evolved considerably. Some of the principles described in this book include the following:

- 23.1. There may be no cortical area in rodents that is homologous to most of the primate including human OFC, its granular cortical regions ([Wise, 2008](#)).
- 23.2. The primate including human OFC implements reward value, as shown by devaluation experiments such as feeding to satiety, and by rapid even rule-based updating of value based on learning.
- 23.3. Value is not represented at earlier stages of processing in primates including humans. Invariant visual object recognition in the inferior temporal visual cortex is used for many functions including memory formation ([Rolls, 2008](#)), so perception is kept separate from emotion.
- 23.4. 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 OFC) and making connections via a pontine taste area present in rodents directly to the hypothalamus and amygdala ([Small & Scott, 2009](#)).
- 23.5. In primates and humans, the OFC 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 OFC may be one computation that granular PFC facilitates. Rodents may not be able to perform this.
- 23.6. The value representation in the primate and human OFC 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](#)). This may not be the case in rodents.
- 23.7. Goal value-directed choice is usual in primates and humans, whereas fixed action patterns, such as pecking in birds, are more common elsewhere.
- 23.8. Goal-directed choice may be the best measure of value and emotion, for there are many partly separate neural circuits for other, different, but emotion-related, responses, e.g., autonomic output, freezing, fixed action patterns, and unconditioned approach or withdrawal.
- 23.9. 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.

3. Comparison with some other approaches to emotion and decision-making

Emotion and Decision-Making Explained is I believe unique as a book in aiming to link understanding of the evolutionary adaptive value and brain mechanisms underlying emotion, to neuroeconomic approaches to valuation, and then beyond this, once value has been assessed, to the neurophysiological mechanisms involved in taking decisions.

Emotion and Decision-Making Explained does provide comparisons with some of the other approaches taken in each of these areas, and a brief overview is provided here to help draw out how the approach in *Emotion and Decision-Making Explained* is different from some other approaches.

Damasio has suggested in his somatic marker hypothesis of emotion (Damasio, 1996) that the insula and related somatosensory cortical areas play a crucial role in emotion and decision-making, by receiving feedback from the periphery that results in an emotion-related decision being made. A quotation from Damasio (1994) (p. 190) follows: “The squirrel did not really think about his various options and calculate the costs and benefits of each. He saw the cat, was jolted by the body state, and ran.” The alternative view proposed in *Emotion and Decision-Making Explained* is that where and how the reward and punishment value of stimuli is decoded is the more fundamental question, that this occurs in the OFC and the amygdala which are the appropriate part of the brain for outputs to influence behaviour (via, e.g., the orbitofrontal to cingulate cortex and orbitofrontal-to-striatal connections), and that the OFC and amygdala, and brain structures that receive connections from them, are the likely places where neuronal activity is directly related to emotional states and to felt emotions, and that feedback from the periphery, the body, would merely introduce signal loss and noise into the decision-making process, and is not consistent with the empirical evidence [see also Maia and McClelland (2004)].

LeDoux (1992, 1995, 1996, 2012) has described a theory of the neural basis of emotion that is probably conceptually similar to that of Rolls (1990, 1999, 2000, 2005, 2013b, 2014b, 2014a), except that LeDoux focuses mostly on the role of the amygdala in emotion (and not on other brain regions such as the OFC, which are poorly developed in the rat); and except that he focuses mainly on fear (based on his studies of the role of the amygdala and related structures in fear conditioning in the rat). Further, LeDoux suggests from his neurophysiological findings that an important route for conditioned emotional stimuli to influence behaviour is via the subcortical inputs (especially auditory from the medial part of the medial geniculate nucleus of the thalamus) to the amygdala, whereas I suggest that cortical processing to the object representation level before the representation is then sent to areas such as the amygdala and OFC is normally involved in emotion, as emotions normally occur to objects, faces, etc. and not to spots of light or pure tones, which is what are represented precortically. Further, LeDoux (2012) has emphasized especially reflexes and conditioned reflexes such as autonomic responses and freezing, which I argue have adaptive value or in LeDoux’s words survival value, but do not involve intervening states such as representations of goals for actions (i.e.,

instrumental reinforcers), and which my theory suggests are emotional states.

Panksepp’s approach to emotion has its origins in neuro-ethological investigations of brainstem systems that when activated lead to behaviours like fixed action patterns, including escape, flight and fear behaviour (Panksepp, 1998, 2011a, 2011b). Using evidence from brain stimulation that elicits behaviours, he has postulated that there is a set of basic emotions, including for example Seeking, Rage, Fear, Lust, Care, Panic/Grief and Play. He argued that these are ‘natural kinds’, things that exist in nature as opposed to being inventions (constructions) of the human mind. My view is that there are not a few basic emotions, that fixed action patterns are not fundamental to emotional states as fixed action patterns do not require intervening emotional states to support goal-directed instrumental actions, and that emotions can be classified based on the specific reinforcer, the specific reinforcement contingency, the actions that are available, etc. (Rolls, 2014a).

These comparisons show that Rolls’ theory of emotion and its brain mechanisms is different from some other theories, is linked to concepts of value in neuroeconomics, argues that value representations provide the goals for instrumental actions and require intervening emotional states, is linked to approaches to understanding how decision-making is implemented in the brain, and does take into account emotion-related decision-making processes versus reasoning decision-making processes that involve multistep one-off planning.

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