

## Emotion and reasoning in human decision-making

*Edmund T. Rolls*

### Abstract

Two systems in the brain that are involved in emotional and economic decision-making are described. The first is an evolutionarily old emotion-based system that operates on rewards defined by the genes such as food, warmth, social reputation, and having children. Such decisions are often based on heuristics, such as being highly sensitive to losses, because a single loss might influence one's reproductive success. This is a multidimensional system with many rewards and punishers, all of which cannot be simultaneously optimized. The second route to decision-making involves reasoning, in which it is assumed that utility can be accurately assessed and logical reason can be applied, though the human brain is not naturally computationally good at logical assessment. When decisions are taken, all those factors apply, and in addition there is noise introduced into the system by the random firing times of neurons for a given mean firing rate. The implications for economic decision-making are described. In macroeconomics, it is assumed that the economy behaves like one “representative” agent who can take rational and logical decisions, and who can maximize utility over a constraint. Given the neuroscience of decision-making, the situation is more complex. The utility function may be multidimensional, the reward value along each dimension may fluctuate, the reasoning may be imperfect, and the decision-making process is subject to noise in the brain, making it somewhat random from occasion to occasion. Moreover, each individual has a different set of value functions along each dimension, with different sensitivities to different rewards and punishers, which are expressed in the different personalities of different individuals. These factors underlying the neuroscience of human decision-making need to be taken into account in building and utilizing macroeconomic theories.

(Published in Special Issue [Bio-psycho-social foundations of macroeconomics](#))

**JEL** D01 D87 D91 E71 G41

**Keywords** Decision-making; brain mechanisms; probabilistic choice; attractor network; reward value; economic value; macroeconomics; microeconomics; orbitofrontal cortex

### Authors

*Edmund T. Rolls*, Oxford Centre for Computational Neuroscience, Oxford, UK;  
University of Warwick, Coventry, UK, [Edmund.Rolls@oxcns.org](mailto:Edmund.Rolls@oxcns.org)

**Citation** Edmund T. Rolls (2019). Emotion and reasoning in human decision-making. *Economics: The Open-Access, Open-Assessment E-Journal*, 13 (2019-39): 1–31. <http://dx.doi.org/10.5018/economics-ejournal.ja.2019-39>

Received February 2, 2019 Published as Economics Discussion Paper February 6, 2019

Revised July 26, 2019 Accepted September 16, 2019 Published October 1, 2019

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## **1 Introduction**

In this article I unravel some of the implications for economics of our understanding of the brain mechanisms underlying valuation and decision-making. I argue that the concept of a rational self-interested decision-maker in economics can now be updated to take into account a much broader perspective on how humans take value-based decisions. The approach taken here to economics complements some other approaches (Glimcher, 2011; Glimcher and Fehr, 2013).

A central issue in this article is how subjective utility is determined, and the factors that influence it. In economics, subjective utility may be inferred from choices. But choices provide information about the ordering of goods (on an ordinal scale), not about their numerical value (on a cardinal scale), so are an imperfect way of measuring utility (Glimcher, 2011). Here I address some of the factors that provide the foundation for a continuous representation in the brain of the subjective utility of ‘goods’, and then how that provides an input to a choice mechanism.

Is subjective utility for the good of the “self-interested” individual? I will argue that what is good for genes also influences utility. Is subjective utility logical, that is, based on estimates of probabilities followed by calculations based on these? I will argue that there are two major systems in our brains that are involved in choices, one that can operate logically or rationally in this way, but a second that operates emotionally, based on gene-specified reinforcers for actions, that is much less calculating, but that reflects factors that have tended to promote survival in our evolutionary history and therefore have been the subject of natural selection. Is subjective utility deterministic? (Note that rational has a technical sense in economics, meaning consistency of choice or preference (Glimcher, 2011)). In Expected Utility theory (von Neumann and Morgenstern, 1944), a chooser has a monotonic utility function in which utility increases with value, and computes the desirability of a lottery by multiplying the probability of the gains or losses by the utility of those gains or losses (Glimcher, 2011). In this article, I use rationality in its neuroscience sense, to indicate reasoning using a syntactic (language-based) system (Rolls, 2007, 2011, 2014, 2016, 2018). I will argue that choice mechanisms in the brain are inherently non-deterministic, and are stochastic, as they are influenced by the randomness in the spiking times of neurons in the brain. I show that the brain’s non-deterministic choice decision systems have evolutionary advantage (Rolls and Deco, 2010; Rolls, 2016). Understanding these factors that influence subjective utility, and the underlying mechanisms that implement choice within the brain, can improve our understanding of utility, that is, what makes us choose particular goods.

## **2 Dual routes to action**

### **2.1 A reward/punishment system for instrumental learning and emotion**

I have presented evidence that there are two types of route to action performed in relation to value, to reward or punishment, in humans (Rolls, 2011, 2012a, 2014, 2016, 2018, 2019c).

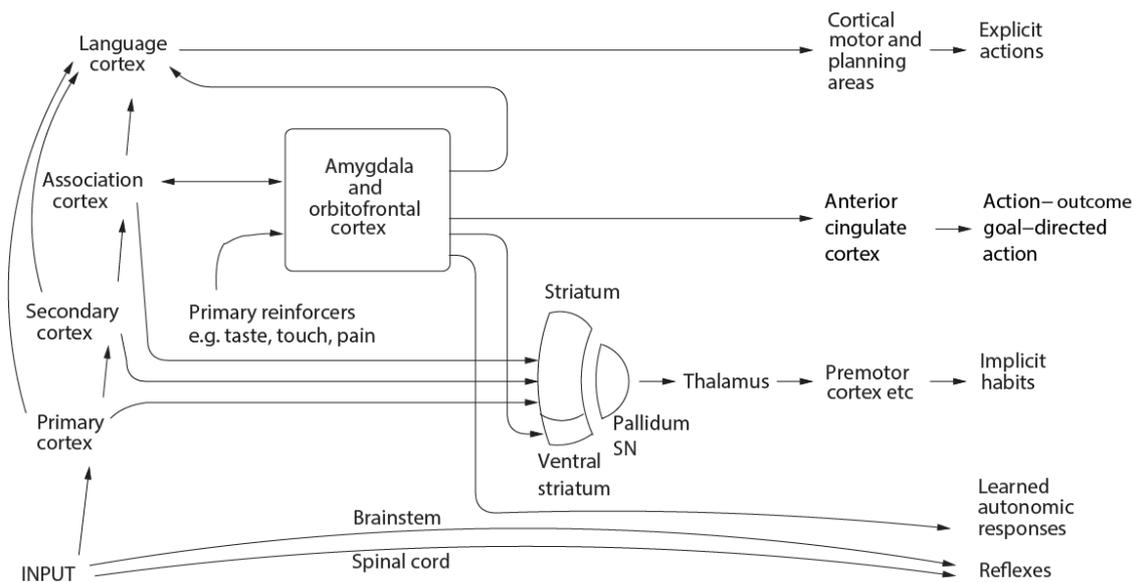
Examples of such actions include emotional and motivational behaviour, and the types of decision and action studied in economics.

The first route is via the brain systems that have been present in non-human primates such as monkeys, and to some extent in other mammals, for millions of years. These systems include the amygdala and, particularly well-developed in primates, the orbitofrontal cortex. These systems control behaviour in relation to reward and punishment as specified by genes as the goals for action. A reward is a stimulus for which an individual will work (i.e. for which actions will be performed that are instrumental in obtaining the reward: instrumental learning), and a punisher is a stimulus that an individual will work to escape from or avoid. Learning allows other previously neutral stimuli to become goals for action by associative learning: secondary reinforcers are learned, and unlearned, because of their relation to primary reinforcers (Rolls, 2014, 2018). (I have noted that specification by genes in this way does not imply genetic determinism: there are many genes competing to promote different actions, the choices are noisy, that is probabilistic, because of noise in the brain, and individual genes can be thought of as influencing but not determining behaviour (Rolls, 2012a)).

The computation that controls the action thus involves assessment of the reinforcement-related value of a stimulus (see Rolls, 2014). This assessment may be based on a number of different factors. One is the previous reinforcement history, which involves stimulus-reinforcement association learning using the amygdala, and its rapid updating especially in primates using the orbitofrontal cortex. This stimulus-reinforcement association learning may involve quite specific information about a stimulus, for example of the energy associated with each type of food, by the process of conditioned appetite and satiety (Booth, 1985). A second is the current motivational state, for example whether hunger is present, whether other needs are satisfied, etc. A third factor that affects the computed reward value of the stimulus is whether that reward has been received recently. If it has been received recently but in small quantity, this may increase the reward value of the stimulus. This is known as incentive motivation or the “salted nut” phenomenon. The adaptive value of such a process is that this positive feedback of reward value in the early stages of working for a particular reward tends to lock the organism onto behaviour being performed for that reward. This means that animals that are for example almost equally hungry and thirsty will show hysteresis in their choice of action, rather than continually switching from eating to drinking and back with each mouthful of water or food. This introduction of hysteresis into the reward evaluation system makes action selection a much more efficient process in a natural environment, for constantly switching between different types of behaviour would be very costly if all the different rewards were not available in the same place at the same time. (For example, walking half a mile between a site where water was available and a site where food was available after every mouthful would be very inefficient.) A fourth factor is the computed absolute value of the reward or punishment expected or being obtained from a stimulus, e.g., the sweetness of the stimulus (set by evolution so that sweet stimuli will tend to be rewarding, because they are generally associated with energy sources), or the pleasantness of touch (set by evolution to be pleasant according to the extent to which it brings animals of the opposite sex together, and depending on the investment in time that the partner is willing to put into making the touch pleasurable, a sign which indicates the commitment and value for the partner of the relationship). After the reward value of the stimulus has been assessed in these ways, behaviour is then initiated based on approach towards

or withdrawal from the stimulus. A critical aspect of the behaviour produced by this type of system is that it is aimed directly towards obtaining a sensed or expected reward, by virtue of connections to brain systems such as the basal ganglia and cingulate cortex (Rolls, 2014, 2016) which are concerned with the initiation of actions (see Fig. 1).

Now part of the way in which the behaviour is controlled with this first route is according to the reward value of the outcome. At the same time, the animal may only work for the reward if the cost is not too high. Indeed, in the field of behavioural ecology, animals are often thought of as performing optimally on some cost-benefit curve (Krebs and Kacelnik, 1991; Mobbs et al., 2018). This does not at all mean that the animal thinks about the rewards, and performs a cost-benefit analysis using a lot of thoughts about the costs, other rewards available and their costs, etc. Instead, it should be taken to mean that in evolution, the system has evolved such that the way in which the reward varies with the different energy densities or amounts of food and the delay before it is received, can be used as part of the input to a mechanism that has also been built to track the costs of obtaining the food (e.g., energy loss in obtaining it, risk of predation, etc.), and to then select (given many such types of reward and the associated cost), the current behaviour that provides the most ‘net reward’. Part of the value of having the computation expressed in this reward-minus-cost form is that there is then a suitable “currency”, or net



*Figure 1: Multiple routes to the initiation of actions and responses 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. Pallidum / SN - the globus pallidus and substantia nigra. 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 ventral, visceral, part of the anterior insular cortex) and amygdala.*

reward value, to enable the animal to select the behaviour with currently the most net reward gain (or minimal aversive outcome).

In terms of the operation of this system, *emotions* can be seen as states elicited by the reinforcers and which have a number of useful functions in relation to obtaining the reinforcers such as maintaining continuity of action, and *motivational states* can be seen as states in which a goal is being sought (Rolls, 2014, 2018).

When verbal declarations are made about decisions made in this first system, those verbal declarations may be confabulations, reasonable explanations, or fabrications of reasons why the choice was made. These reasonable explanations would be generated to be consistent with the sense of continuity and self that is a characteristic of reasoning in the language system (Rolls, 2011, 2014, 2016, 2018).

## **2.2 The reasoning, rational, route to action**

The second route in humans involves a computation with many “if ... then” statements, to implement a plan to obtain a reward. In this case, the reward may actually be *deferred* as part of the plan, which might involve working first to obtain one reward, and only then to work for a second more highly valued reward, if this was thought to be overall an optimal strategy in terms of resource usage (e.g., time). In this case, syntax is required, because the many symbols (e.g., names of people) that are part of the plan must be correctly linked or bound. Such linking might be of the form: “if A does this, then B is likely to do this, and this will cause C to do this ...”. The requirement of syntax for this type of planning implies that an output to language systems in the brain is required for this type of planning (see Fig. 1) (Rolls, 2014, 2018). Thus the explicit language system in humans may allow working for deferred rewards by enabling use of a one-off, individual, plan appropriate for each situation.

Another building block for such planning operations in the brain may be the type of short term memory in which the prefrontal cortex is involved. This short term memory may be for example in non-human primates of where in space a response has just been made. A development of this type of short term response memory system in humans to enable multiple short term memories to be held in place correctly, preferably with the temporal order of the different items in the short term memory coded correctly, may be another building block for the multiple step “if .... then” type of computation in order to form a multiple step plan. Such short term memories are implemented in the (dorsolateral and inferior convexity) prefrontal cortex of non-human primates and humans (Goldman-Rakic, 1996; Kolb and Whishaw, 2015; Rolls, 2016), and may be part of the reason why prefrontal cortex damage impairs planning (Shallice and Cipolotti, 2018).

## **3 Decisions between the emotional and reasoning systems**

The question then arises of how decisions are made in animals such as humans that have both the implicit, direct reward-based, and the explicit, rational, planning systems (see Fig. 1) (Rolls,

2011, 2014, 2018). One particular situation in which the first, implicit, system may be especially important is when rapid reactions to stimuli with reward or punishment value must be made, for then the direct connections from structures such as the orbitofrontal cortex to the basal ganglia may allow rapid actions (Rolls, 2014). Another is when there may be too many factors to be taken into account easily by the explicit, rational, planning, system, when the implicit system may be used to guide action. In contrast, when the implicit system continually makes errors, it would then be beneficial for the organism to switch from automatic, direct, action based on obtaining what the orbitofrontal cortex system decodes as being the most positively reinforcing choice currently available, to the explicit conscious control system which can evaluate with its long-term planning algorithms what action should be performed next. Indeed, it would be adaptive for the explicit system to regularly be assessing performance by the more automatic system, and to switch itself in to control behaviour quite frequently, as otherwise the adaptive value of having the explicit system would be less than optimal.

There may also be a flow of influence from the explicit, verbal system to the implicit system, in that the explicit system may decide on a plan of action or strategy, and exert an influence on the implicit system which will alter the reinforcement evaluations made by and the signals produced by the implicit system (Rolls, 2014, 2018).

It may be expected that there is often a conflict between these systems, in that the first, implicit, system is able to guide behaviour particularly to obtain the greatest immediate reinforcement, whereas the explicit system can potentially enable immediate rewards to be deferred, and longer-term, multi-step, plans to be formed. This type of conflict will occur in animals with a syntactic planning ability, that is in humans and any other animals that have the ability to process a series of “if ... then” stages of planning. This is a property of the human language system, and the extent to which it is a property of non-human primates is not yet fully clear. In any case, such conflict may be an important aspect of the operation of at least the human mind, because it is so essential for humans to correctly decide, at every moment, whether to invest in a relationship or a group that may offer long-term benefits, or whether to directly pursue immediate benefits (Rolls, 2014, 2018).

The thrust of the argument (Rolls, 2014, 2018) thus is that much complex animal including human behaviour can take place using the implicit, non-conscious, route to action. We should be very careful not to postulate intentional states (i.e., states with intentions, beliefs and desires) unless the evidence for them is strong, and it seems to me that a flexible, one-off, linguistic processing system that can handle propositions is needed for intentional states. What the explicit, linguistic, system does allow is exactly this flexible, one-off, multi-step planning ahead type of computation, which allows us to defer immediate rewards based on such a plan.

This discussion of dual routes to action has been with respect to the behaviour produced. There is in addition a third output of brain regions such as the orbitofrontal cortex and amygdala involved in emotion, that is directed to producing autonomic and endocrine responses (see Fig. 1). Although it has been argued by Rolls (2014) that the autonomic system is not normally in a circuit through which behavioural responses are produced (i.e., against the James-Lange and related somatic theories), there may be some influence from effects produced through the endocrine system (and possibly the autonomic system, through which some endocrine responses are controlled) on behaviour, or on the dual emotional and rational systems just discussed that control behaviour.

## **4 The selfish gene vs the selfish phene**

I have provided evidence above that there are two main routes to decision-making and action. The first route selects actions by gene-defined goals for action, and is closely associated with emotion. The second route involves multistep planning and reasoning which requires syntactic processing to keep the symbols involved at each step separate from the symbols in different steps. (This second route is used by humans and perhaps by closely related animals.) Now the ‘interests’ of the first and second routes to decision-making and action are different. As argued very convincingly by Richard Dawkins in *The selfish gene* (Dawkins, 1989), and by others (Hamilton, 1964; Ridley, 1993; Hamilton, 1996), many behaviours occur in the interests of the survival of the genes, not of the individual (nor of the group), and much behaviour can be understood in this way. I have extended this approach by arguing that an important role for some genes in evolution is to define the goals for actions that will lead to better survival of those genes; that emotions are the states associated with these gene-defined goals; and that the defining of goals for actions rather than actions themselves is an efficient way for genes to operate, as it leaves flexibility of choice of action open until the animal is alive (Rolls, 2014, 2018). This provides great simplification of the genotype as action details do not need to be specified, just rewarding and punishing stimuli, and also flexibility of action in the face of changing environments faced by the genes. Thus the interests that are implied when the first route to action is chosen are those of the “selfish genes”, not those of the individual.

However, the second route to action allows, by reasoning, decisions to be taken that might not be in the interests of the genes, might be longer term decisions, and might be in the interests of the individual. An example might be a choice not to have children, but instead to devote oneself to science, medicine, music, or literature. The reasoning, rational, system presumably evolved because taking longer-term decisions involving planning rather than choosing a gene-defined goal might be advantageous at least sometimes for genes. But an unforeseen consequence of the evolution of the rational system might be that the decisions would, sometimes, not be to the advantage of any genes in the organism. After all, evolution by natural selection operates utilizing genetic variation like a Blind Watchmaker (Dawkins, 1986). In this sense, the interests when the second route to decision-making is used are at least sometimes those of the “selfish phenotype”. (Indeed, we might euphonicly say that the interests are those of the “selfish phene” (where the etymology is Gk *phaino*, ‘appear’, referring to appearance, hence the thing that one observes, the individual). Hence the decision-making referred to above is between a first system where the goals are gene-defined, and a second rational system in which the decisions may be made in the interests of the genes, or in the interests of the phenotype and not in the interests of the genes. Thus we may speak of the choice as sometimes being between the “selfish genes” and the “selfish phenes”.

Now what keeps the decision-making between the “selfish genes” and the “selfish phenes” more or less under control and in balance? If the second, rational, system chose too often for the interests of the “selfish phene”, the genes in that phenotype would not survive over generations. Having these two systems in the same individual will only be stable if their potency is approximately equal, so that sometimes decisions are made with the first route, and sometimes with the second route. If the two types of decision-making, then, compete with approximately equal potency, and sometimes one is chosen, and sometimes the other, then this is exactly the

scenario in which stochastic processes in the decision-making mechanism are likely to play an important role in the decision that is taken (Rolls, 2014, 2016). The same decision, even with the same evidence, may not be taken each time a decision is made, because of noise in the system.

The system itself may have some properties that help to keep the system operating well. One is that if the second, rational, system tends to dominate the decision-making too much, the first, gene-based emotional system might fight back over generations of selection, and enhance the magnitude of the reward value specified by the genes, so that emotions might actually become stronger as a consequence of them having to compete in the interests of the selfish genes with the rational decision-making process.

Another property of the system may be that sometimes the rational system cannot gain all the evidence that would be needed to make a rational choice. Under these circumstances the rational system might fail to make a clear decision, and under these circumstances, basing a decision on the gene-specified emotions is an alternative. Indeed, Damasio (1994) argued that under circumstances such as this, emotions might take an important role in decision-making. In this respect, I agree with him, basing my reasons on the arguments above. He called the emotional feelings gut feelings, and, in contrast to me, hypothesized that actual feedback from the gut was involved. His argument seemed to be that if the decision was too complicated for the rational system, then send outputs to the viscera, and whatever is sensed by what they send back could be used in the decision-making, and would account for the conscious feelings of the emotional states. My reading of the evidence is that the feedback from the periphery is not necessary for the emotional decision-making, or for the feelings, nor would it be computationally efficient to put the viscera in the loop given that the information starts from the brain, but that is a matter considered elsewhere (Maia and McClelland, 2004; Rolls, 2014, 2018).

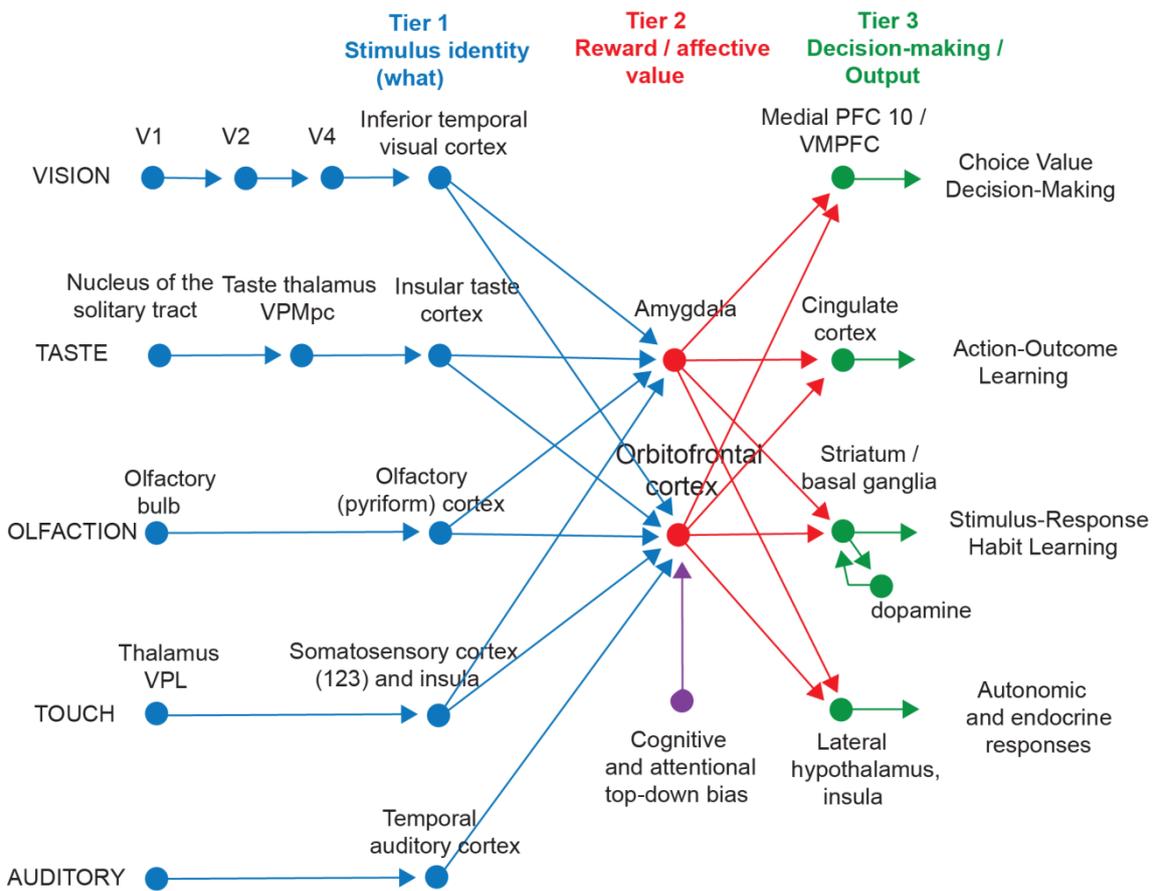
Another property of the system is that the interests of the second, rational, system, although involving a different form of computation, should not be too far from those of the gene-defined emotional system, for the arrangement to be stable in evolution by natural selection. One way that this could be facilitated would be if the gene-based goals felt pleasant or unpleasant in the rational system, and in this way contributed to the operation of the second, rational, system. This is something that I propose is the case (Rolls, 2011, 2014, 2018).

## **5 The value or reward system in the brain, and its relation to emotion: a second tier after the perceptual representation**

An outline of the pathways involved in *taste, olfactory, visual and somatosensory and also abstract monetary* reward is shown in Fig. 2 (Rolls and Grabenhorst, 2008; Grabenhorst and Rolls, 2011; Rolls, 2014, 2018, 2019c). Conceptually, the orbitofrontal cortex and amygdala in the column labelled ‘reward’ in Fig. 2 in which reward value is represented can be thought of as receiving from the ends of each modality-specific cortical pathway in which the identity of each sensory stimulus is represented independently of its reward value. These areas in which the identity of each stimulus is represented (what visual object or face, what taste, what flavour,

what odour etc) is shown by the column in Fig. 2 with inferior temporal visual cortex, primary taste cortex in the anterior insula, pyriform olfactory cortex, and somatosensory cortex.

Part of the utility of this functional architecture is that there is a representation of what stimulus is present that is independent of its reward value, so that learning to associate that stimulus with its spatial position, to recognise and name it, and learn about its properties can occur independently of its current affective value (Rolls, 2014, 2018, 2019c). A simple example is that we can learn about the location of a food even if we are not hungry and it has no reward value. At the subjective level, we can report on the properties and intensity of stimuli independently of whether they are currently pleasant. A computational principle is thus that there are separate representations of what a stimulus is together with its intensity, and its



*Figure 2:* 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. The Medial PFC area 10 is part of the ventromedial prefrontal cortex (VMPFC). 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. 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 / affective 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. A pathway for top-down attentional and cognitive modulation of emotion is shown in purple. Auditory inputs also reach the amygdala.

affective value. Some computational reasons for this segregation into different areas are described later.

The evidence that reward is represented in structures such as the orbitofrontal cortex and a region to which it connects the anterior cingulate cortex (including the pregenual cingulate cortex for rewards and the more dorsal cingulate regions for unpleasant stimuli (Grabenhorst and Rolls, 2011; Rolls, 2019c) is that representations of food related stimuli in these regions only occur when food is rewarding because hunger is present and not when the food is no longer rewarding because it has been eaten satiety; and that activations in these regions correlate with the subjective pleasantness of the stimuli. Monetary reward is represented in these regions, in that activations in the medial orbitofrontal cortex correlate with the amount of reward won on each trial, and in the lateral orbitofrontal cortex with the amount of money lost on a trial (O'Doherty et al., 2001; Rolls, 2019c). The representations of many different rewards are grouped together in the medial orbitofrontal cortex, and this may provide a mechanism for them to be compared by competitive interactions implemented by lateral inhibition (Rolls and Grabenhorst, 2008; Rolls, 2009b, 2014, 2018, 2019c). It is fundamental though that each reward is represented by its own computationally independent though distributed subpopulation of neurons so that each type of reward is separate from the other rewards, and each can be a goal for a separate action (Rolls and Grabenhorst, 2008; Rolls, 2009b, 2014, 2018, 2019c).

Inputs that are not primary (unlearned, gene-specified) reinforcers, such as most visual stimuli, can become secondary (learned) reinforcers by *associative learning* with primary reinforcers (such as taste, punishing including painful, and thermal stimuli) in the orbitofrontal cortex. The visual input is from the ventral, temporal lobe, visual stream concerned with “what” object is being seen (Rolls, 2000; Rolls, 2012b; Rolls, 2016). Many of these neurons show visual-taste reversal of associations in one or a very few trials. 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., 1996; Rolls, 2019c). The probable mechanism for this learning is an associative modification of synapses conveying visual input onto neurons responding to primary reinforcers, implementing a pattern association network (Rolls and Treves, 1998; Rolls, 2014, 2016, 2018, 2019c).

*Social reinforcers* such as face and voice expression are also represented in the orbitofrontal cortex (Thorpe et al., 1983; Kringelbach and Rolls, 2003; Rolls et al., 2006). The significance of these 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; Rolls, 2019c) (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 utilising learned reinforcing inputs in social situations e.g., about the current reinforcement value as decoded by stimulus-reinforcement association to a particular individual.

*Top-down effects of cognition and attention on the value of stimuli*, very important in our economic valuation processes, are implemented in the orbitofrontal cortex value representations. For example, verbal descriptions of the value of stimuli can bias the activations to incoming

(bottom-up) olfactory, taste and tactile stimuli (de Araujo et al., 2005; Grabenhorst et al., 2008a; McCabe et al., 2008; Rolls, 2014, 2018, 2019c). What may be a fundamental principle for how top-down attention can influence affective vs non-affective processing has recently been discovered. For an identical taste stimulus, paying attention to pleasantness activates brain systems in the affective stream including the orbitofrontal and pregenual cingulate cortex, and paying attention to intensity, which reflected the physical and not the affective properties of the stimulus, activated brain areas in the discriminative (“what” or object) stream (Grabenhorst and Rolls, 2008). The same occurs for olfactory processing (Rolls et al., 2008b). The mechanism is biased activation (Deco and Rolls, 2005; Grabenhorst and Rolls, 2010; Rolls, 2016). The implication is that different types of choice mechanism during economic decision-making will be engaged depending on whether attention is to the reward value or some other discriminative property of the stimulus.

Approaches used in neuroeconomics (Glimcher and Fehr, 2013) help to define further the nature of the representation of reinforcers in the orbitofrontal cortex. When monkeys choose between different numbers of drops of two juices, one more preferred than the other, some neurons in the orbitofrontal cortex encode the offer value, some the choice value, and some the taste, but not the details of the motor response that is chosen (Padoa-Schioppa and Assad, 2006). Further, these neurons encode economic value, not relative preference, as shown by a study in which a particular reward was paired with other rewards. The fact that the neuronal responses are menu invariant suggests that transitivity, a fundamental trait of economic choice, may be rooted in the activity of individual neurons (Padoa-Schioppa and Assad, 2008; Padoa-Schioppa and Conen, 2017). There is also evidence that relative reward value may be represented in the orbitofrontal cortex (Tremblay and Schultz, 1999), and in what may provide a resolution of this, we have found that some parts of the orbitofrontal cortex may represent the absolute pleasantness of stimuli and others the relative pleasantness of stimuli (Grabenhorst and Rolls, 2009). The representation of absolute value is important for long-term rational economic choice, and of relative reward value for the choice between two or more rewards on a particular trial (Grabenhorst and Rolls, 2009; Rolls, 2014, 2019c).

When a choice is made between stimuli with different reward probabilities, that is under conditions of *uncertainty*, the choice made depends on the probability with which each reward will be obtained. In this probabilistic decision-making situation, we can define *expected value as probability  $\times$  reward magnitude* (Glimcher, 2004; Rolls, 2014). In an fMRI investigation of such a probabilistic choice decision task in which humans chose between two rewards each available with different probabilities, it was found that the activation of the orbitofrontal cortex was related to expected value while the decision was being made, and also to the reward magnitude announced later on each trial (Rolls et al., 2008a). An implication is that in situations where decisions are made under conditions of *uncertainty*, the part of the brain that represents the magnitude of the reward obtained on each trial (the orbitofrontal cortex (O’Doherty et al., 2001; Rolls and Grabenhorst, 2008; Rolls et al., 2008a)) also contains a representation that could just be the reward magnitude weighted by the average over recent history of the reward obtained on a typical trial when that conditioned stimulus is shown. This is a simple way in which expected value could be computed in the orbitofrontal cortex as the probability of obtaining a reward on a given trial multiplied by the reward magnitude on a trial in which a reward is obtained (Rolls et al., 2008a; Rolls, 2014). Further evidence in a variety of tasks

implicates a related and partly overlapping region of the ventromedial prefrontal cortex with positive expected value (Fouragnan et al., 2018). In contrast, the reward prediction errors or temporal difference errors as defined in reinforcement learning (Sutton and Barto, 1998; Schultz, 2016) are usually evident in the ventral striatum in imaging studies (Rolls et al., 2008a; Fouragnan et al., 2018), though we should remember that such signals may be generated in the orbitofrontal cortex (Rolls and Grabenhorst, 2008; Rolls, 2014; Rolls, 2017; Rolls, 2018, 2019c), in that negative *reward prediction errors* are represented by error neurons in the primate orbitofrontal cortex (Thorpe et al., 1983), in that the lateral orbitofrontal cortex is activated when a negative reward prediction error is generated in the reversal of a visual discrimination task (Kringelbach and Rolls, 2003), and in that damage to the orbitofrontal cortex impairs the ability to respond to negative reward prediction error (Rolls et al., 1994; Rolls, 1999b; Hornak et al., 2004; Rolls, 2019c).

Although it might be anticipated that the actual utility or ‘subjective utility’ of an offer (a choice) to an individual approximately tracks the expected value, this is not exactly the case, with subjects typically undervaluing high rewards, and being over-sensitive to high punishments (Bernoulli, 1738 / 1954; von Neumann and Morgenstern, 1944; Kahneman and Tversky, 1979; Kahneman and Tversky, 1984; Tversky and Kahneman, 1986; Gintis, 2000; Rangel et al., 2008; Glimcher and Fehr, 2013). Part of the adaptive value of being especially sensitive to punishments is that even a single aversive event might be life and gene-threatening (and might damage an individual’s reputation, or ability to compete in intrasexual competition), whereas missing some possible rewards is likely to have much less serious consequences. Subjects also typically have a subjective utility function that discounts rewards the further in the future they are delayed (McClure et al., 2004; Glimcher and Fehr, 2013). Some parts of the ventromedial prefrontal cortex have activations that may follow the subjective utility, of for example delayed rewards. In a study of this, it was found that activations in the ventromedial prefrontal cortex were correlated with the subjective utility of rewards delayed for different times, with the discount curve for each subject reconstructed from each subject’s choices (Kable and Glimcher, 2007).

These representations of *value on a continuous scale* (separate scalar variables for each type of reward) are the input to a third tier of processing, that involved in making choices between rewards (Rolls, 2019c).

## **6 Choice decision-making in the brain: a third tier**

### **6.1 A third cortical tier implicated in choice decision-making**

A representation of reward magnitude, expected value, and even the subjective utility of a reward is an important input to a decision-making process, and the orbitofrontal cortex appears to provide this information (Rolls, 2019c). When making a decision between two rewards, or whether to work for a reward that has an associated cost, it is important that the exact value of each reward is represented and enters the decision-making process. However, when a decision is reached, a system is needed that can make a binary choice, so that on one trial the decision

might be reward 1, and on another trial reward 2, so that a particular action can be taken. For the evaluation, the neural activity needs to represent a stimulus in a way that continuously and faithfully represents the affective or reward value of the stimulus, and this could be present independently of whether a binary choice decision is being made or not. On the other hand, when a binary (choice) decision must be reached, a neural system is needed that does not continuously represent the reward value of the stimulus, but which instead falls into a binary state, in which for example the high firing of some neurons represents one decision (i.e. choice), and the high firing of other neurons represents a different choice. Processes such as this transition from spontaneous firing to a binary state of firing of neurons (fast vs slow) are known to occur in some premotor and related areas such as the macaque ventral premotor cortex when decisions are taken, about in this case which vibrotactile stimulus to choose (Deco et al., 2013; Rolls, 2016).

It has been proposed that there may be a similar binary choice system, in another brain region, that becomes engaged when choice decisions are between rewards, or about rewards with which there is an associated cost (Rolls, 2014, 2019c). To investigate whether representing the affective value of a reward on a continuous scale may occur before and separately from making a binary, for example yes-no, decision about whether to choose the reward, Grabenhorst et al (2008b) used fMRI to measure activations produced by pleasant warm, unpleasant cold, and affectively complex combinations of these stimuli applied to the hand. On some trials the affective value was rated on a continuous scale, and on different trials a Yes-No (binary choice) decision was made about whether the stimulus should be repeated in future. Activations that were continuously related to the pleasantness ratings and that were not influenced when a binary (choice) decision was made were found in the orbitofrontal and pregenual cingulate cortex, implicating these regions in the continuous representation of affective value, consistent with the evidence described above. In this study, decision-making contrasted with just rating the affective stimuli revealed activations in the medial prefrontal cortex area 10, implicating this area in choice decision making (Grabenhorst et al., 2008b).

Support for a contribution of medial prefrontal cortex area 10 (with an alternative term 'ventromedial prefrontal cortex', VMPFC (Rolls, 2019c)) to taking binary (choice) decisions comes from a fMRI study in which two odors were separated by a delay, with instructions on different trials to decide which odor was more pleasant, or more intense, or to rate the pleasantness and intensity of the second odor on a continuous scale without making a binary (choice) decision. Activations in the medial prefrontal cortex area 10, and in regions to which it projects including the anterior cingulate cortex and insula, were higher when binary choice decisions were being made compared to making ratings on a continuous scale, further implicating these regions in choice decision-making (Rolls et al., 2010b).

Different brain systems were implicated in different types of choice decision-making (Rolls et al., 2010b; Rolls, 2014). Decision-making about the affective value of odors produced larger effects in the dorsal part of medial prefrontal cortex area 10 and the agranular insula, whereas decisions about intensity produced larger effects in the dorsolateral prefrontal cortex, ventral premotor cortex, and anterior insula.

Consistent with these findings, patients with medial prefrontal cortex lesions are impaired in a decision-making shopping task, as reflected for example by visits to previously visited

locations (Gilbert and Burgess, 2008; Shallice and Cipolotti, 2018). In another imaging study, area 10 activation has been related to moral decision-making (Heekeren et al., 2005).

In the study with warm and cold stimuli, and mixtures of them, when a (choice) decision was yes vs no, effects were found in the dorsal anterior cingulate cortex (Grabenhorst et al., 2008b), an area implicated by many other studies in decision-making (Behrens et al., 2007; Marsh et al., 2007). The anterior cingulate cortex has been implicated in action-outcome learning (Rushworth et al., 2012; Rolls, 2019c), and the study with warm and cold stimuli shows that the contribution of the anterior cingulate cortex is in the choice decision-making itself, and that its activation does not occur just in relation to the pleasantness or intensity of the stimuli (Grabenhorst et al., 2008b).

## **6.2 The mechanism for choice decision-making, and noise in the system resulting in probabilistic decision-making**

Attractor networks implemented by the recurrent collateral connections between cortical pyramidal cells provide a way to understand choice decision-making in the brain and its probabilistic nature (Wang, 2002; Deco and Rolls, 2006; Deco et al., 2009; Rolls and Deco, 2010; Deco et al., 2013; Rolls, 2014, 2016). Each set of neurons in the network that if in the high firing rate state represents one of the attractors corresponds to one of the decisions, and is biased on by the evidence for that decision, which might be the reward outcome expected if that decision is taken (i.e. the expected value) (see Fig. 3). Because of the inhibitory interneurons, only one high firing rate attractor state can be active at any one time, so a choice is made on each trial. The state reached on a trial, i.e. the decision taken, depends on the relative strength of the different expected rewards, and on the noise within the network caused by the almost random (Poisson) spiking times for a given mean rate of the neurons in the network (see Fig. 3).

The fact that internal noise in the decision-making systems in the brain can make the decision-making probabilistic and non-deterministic, with possibly different decisions on different trials, is important for economics. The economic person cannot be considered in this respect as a rational self-interested individual: the decision-making is probabilistic (Rolls and Deco, 2010; Rolls, 2014, 2016). Moreover, a probabilistic decision-making network is also involved with choice made between decisions based on activity in the reward-related and rational systems (Rolls and Deco, 2010; Rolls, 2019c).

## **6.3 Confidence in decisions, and the monitoring and correction of decisions before the outcome is known**

When an attractor network makes a decision, the firing rate of the winning attractor will be a little higher if the external evidence is consistent with the noise-influenced decision reflected by the firing supported by the excitatory recurrent collateral connections, and a little lower if the external evidence is inconsistent with the decision made. The reason for this is that the external inputs add to the firing generated internally by the recurrent collateral feedback connections

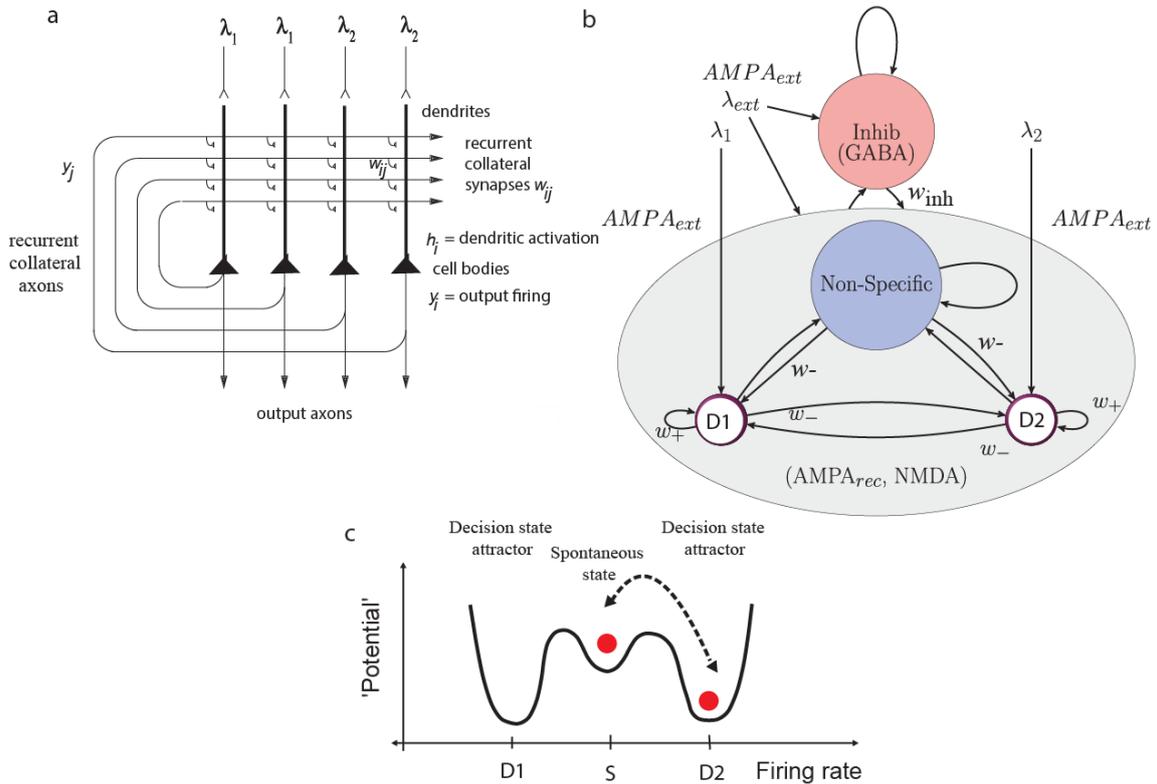


Figure 3: (a) Attractor or autoassociation single network architecture for decision-making. The cell body of each neuron is shown as a triangle (like a cortical pyramidal cell), the dendrite is vertical, and receives recurrent collateral synaptic connections  $w_{ij}$  from the other neurons. The evidence for decision 1 is applied via the  $\lambda_1$  inputs, and for decision 2 via the  $\lambda_2$  inputs. The synaptic weights  $w_{ij}$  have been associatively modified during training in the presence of  $\lambda_1$  and at a different time of  $\lambda_2$ . When  $\lambda_1$  and  $\lambda_2$  are applied, each attractor competes through the inhibitory interneurons (not shown), until one wins the competition, and the network falls into one of the high firing rate attractors that represents the decision. The noise in the network caused by the random spiking of the neurons means that on some trials, for given inputs, the neurons in the decision 1 (D1) attractor are more likely to win, and on other trials the neurons in the decision 2 (D2) attractor are more likely to win. This makes the decision-making probabilistic, for, as shown in (c), the noise influences when the system will jump out of the spontaneous firing stable (low energy) state S, and whether it jumps into the high firing state for decision 1 (D1) or decision 2 (D2). (b) The architecture of the integrate-and-fire network used to model decision-making (see text). (c) A multistable “effective energy landscape” for decision-making with stable states shown as low “potential” basins. Even when the inputs are being applied to the network, the spontaneous firing rate state is stable, and noise provokes transitions into the high firing rate decision attractor state D1 or D2 (see Rolls and Deco 2010).

(see Fig. 3) (Rolls and Deco, 2010; Rolls et al., 2010c; Rolls, 2016). Now confidence in a decision and the mechanism just described shows how confidence is an emergent property of the decision-making network described, and is reflected in the firing rate of the winning attractor, from which confidence can be read out (Rolls, 2016). This makes predictions about the neuroimaging BOLD signals during decision-making, and these predictions have been tested and confirmed for the area implicated in value-related decision-making, the medial prefrontal cortex area 10 (Rolls et al., 2010c). Correspondingly, if the decision made is incorrect, in error, confidence is lower and the firing rates of the winning attractor are lower. The fMRI predictions have also been confirmed (Rolls et al., 2010a). Both studies provide support to value-based

decision-making mechanisms described here, show how confidence in decisions probably arises, and what it actually reflects in the brain (Rolls, 2014, 2016).

Given these concepts, we have shown that a second decision-making network can follow the first, and take a decision about whether to continue with a strategy, or abort the previous decision and try again (Insabato et al., 2010). The second network bases its decisions on the firing rates in the first decision-making network, which encode confidence in the first decision. Thus monitoring of choices even before outcomes are known, and correcting previous decisions if appropriate, is a process that can be understood by simple processes in the brain.

The implication for economics is that decisions can be influenced by noise in the brain; that confidence can be read out from the decision-making network itself; that the decisions on different trials may be different because of noise influencing whether the rational or the emotional system dominates; that checks on decisions should therefore always be made; that a second network monitoring the confidence-related firing rates of a first decision-making network provides one mechanism for correcting previous decisions, though further checking by the rational decision-making system may be useful; and that the rational decision-making system should not always trust what may be confabulations if a decision has been made based on activity in the emotional system (Rolls and Deco, 2010; Rolls, 2011, 2014, 2016).

#### **6.4 Cortical networks that make choices between rewards: Is there a common currency?**

In decision-making between rewards, the different inputs are the different rewards (Fig. 3). One input might be an expected taste reward, another an expected monetary reward, another a social reward. Some authors have talked about a common currency for rewards (McFarland, 1989; Montague and Berns, 2002; Izuma et al., 2008; Sescousse et al., 2015). What might this mean with this type of neuronal processing? In the neuronal decision mechanism described, the decision state is high firing activity of the representation of the particular reward that has won. This is excellent, because then action systems are provided with the information about the particular reward that is the goal of the action, and of course the actions selected will have to depend on the goal that has been selected. The fact that it is an attractor network that represents the reward selected is also very useful, for the short term memory properties of the attractor network will keep the goal representation active while an action is being selected and performed. We can note that it would not be at all helpful to change the rewards into a common currency (such as points, or dollars) as part of the selection process, as this would leave the selected goal just a number of points, or a number of dollars, which would not be useful to guide particular actions (Rolls, 2019c).

What is needed is that the different expected rewards that are the inputs to the decision networks must be on approximately the same scale. If food reward were to always be much stronger than other rewards, then the animal's genes would not survive, for it would never drink water, reproduce, etc. It has therefore been suggested that genes that specify rewards must be selected to ensure that the rewards they specify are approximately of the same maximum value, so that they will all be selected at some time (Rolls, 2014, 2018). There are of course factors that modulate the current value of each reward, such as hunger for food reward, thirst for water

reward, etc. Important also in the modulation of the value of each reward is sensory-specific satiety, a property of it is suggested all reward types to help selection of different rewards which in general is adaptive (Rolls, 2014, 2018). The opposite is also a useful principle, namely incentive motivation, the shorter term increase in the reward value of a particular reward after a particular reward has been obtained (or salted nut phenomenon (Hebb, 1949)), which has the adaptive utility of helping behaviour to lock on to a goal for a useful and efficient amount of time, rather than continually switching between rewards (Rolls, 2014, 2018). Thus we might speak of a common scale for different rewards in that each reward type must have a similar maximal value to other rewards as inputs that can drive the attractor decision-making network so that each reward is selected at least sometimes. But there is no need to talk of a common currency in which all specific rewards are converted into a common currency such as points (Rolls, 2019c). We can note that although the rewards that are specified as primary reinforcers by the genes should be specified to be approximately equipotent, learning mechanisms can adjust the reward value of what starts as a primary reinforcer, as when a taste is associated with sickness in taste aversion learning. As we shall see next, the costs associated with each reward can also be a factor.

Now in fMRI studies, it is frequently found that many different reward types (including taste, olfactory, flavour, texture, somatosensory, monetary, face expression, and social reputation rewards) activate rather similar brain areas, which often include the medial orbitofrontal cortex and pregenual cingulate cortex (Izuma et al., 2008; Rolls and Grabenhorst, 2008; Rolls, 2009a, 2014, 2018, 2019b). Does this provide evidence for a common reward representation, of for example points? The evidence is that it does not, for all the single neuron recording studies described above and elsewhere show that specific rewards are represented by each neuron, which often responds to a particular combination of sensory inputs (Rolls and Grabenhorst, 2008; Grabenhorst and Rolls, 2011; Rolls, 2014, 2018, 2019a, c). So why may all these different specific rewards be represented close together in for example the medial orbitofrontal cortex? The answer I suggest is that the implementation of decision-making between rewards by an attractor network means that all the different reinforcers have to be brought spatially close together to compete with each other in a single network. The spatial constraint is that cortical networks operate over a short range of a few mm (for very good computational reasons described by Rolls (2016)), and this is why in this case the different rewards, to compete within the same network using the short range inhibitory interneurons, and to support each other using the short range cortical excitatory recurrent collaterals, need to be represented close together in the cerebral cortex (Rolls, 2016).

How are costs taken into account in this decision-making process between different rewards? I suggest that the costs incurred in obtaining each goal need to be subtracted from the reward value of each goal, before they enter the decision-making network. The reason for this is that the costs are different for each type of reward, and so it could not make sense to choose the best reward independently of the cost of obtaining that reward. And to choose the best reward independent of cost, and then to go through a process of evaluating the cost for the highest reward, then if that does not exceed some criterion moving to the second highest reward, would also be computationally very time-consuming, as well as difficult to implement. For these reasons, the cost specific to each reward should be subtracted from the expected value of that reward to produce a *net value* for that reward-cost pair before the decision-making network that

makes the choice selection (Rolls and Grabenhorst, 2008; Grabenhorst and Rolls, 2011; Rolls, 2014, 2019c). It will be very interesting to discover whether there are such representations of net reward-cost value in the brain, and if they are the inputs to the choice decision-making networks. There is an indication that this can occur in some orbitofrontal cortex neurons (Cai and Padoa-Schioppa, 2019; Rolls, 2019c). An indication that I note is that costs may be dependent on the frequency of choices by others, which might influence the availability of resources.

## **7 Implications for economic choice**

I now consider the implications of this neurobiological approach to economics (Rolls, 2012a, 2014).

I start with the concept that a classical approach taken in economics is to build theories and analyses based on predictions of choices made by self-interested, rational (in its economics sense of consistent (Glimcher, 2011)), individuals. I consider what the interests and values of individuals are in the light of modern neurobiology and neuroscience. I argue that what might be seen in economics as the interests of the individual may not be only those of the person, the phenome (the phenotype, the person with the body). I argue that instead the values of the individual may be shaped in part, and frequently unconsciously, by the values built-in to people by the genome. These gene-based values may not be in the individuals' interests, but in the genes' interests. I thus argue that at least the concept of a self-interested individual in economics needs to be broadened to take into account the fact that what people value, and choose, may not be for their own good, but for their genes' good. When we consider that the gene-based value and emotional systems may influence our choice, frequently in a way that we cannot identify with language and rational description, though about which we may confabulate a description, we may be moving towards a more fundamental reassessment of approaches used in economics. Importantly, because of confabulation, it may be wise not to base our analyses on what people say, or say they will choose. The choices themselves are of course important, but, further, are not necessarily consistent. For example, when we include the fact that our choices are frequently influenced by noise in the brain, and this includes whether a choice on a particular occasion is more influenced by rational thought or by the gene-based emotional system, the new approach to economics based on neurobiology becomes quite radical and new (Rolls, 2012a, 2014, 2019c). The field of neuroeconomics is moving in this direction, but some of the present approach is quite fundamental even with respect to neuroeconomics.

In some of the examples I provided in developing these arguments, it is shown that a gene-based interest may not be consistent with what might be chosen rationally, i.e. by the reasoning system, and for the self-interest of the individual. What is good for the genome may not be good for the rational, self-interested, phenome.

## **7.1 Logic, rationality (reasoning), gene-based choices, and the brain**

The brain is poor at logic. It is not designed with a small number of inputs to each neuron (the computational unit of the brain) between which a logical function (such as AND, NAND, OR) determines the output (which is how digital computers operate). Instead, the brain operates by computing the similarity (correlation, or dot product) between typically a vector of 10,000 input firings from other neurons, and the vector of synaptic weight values, reflecting previous learning, that determine how much influence each synaptic input has on a neuron. This results in a continuously variable (scalar) firing rate of the neuron which is its output. This is the way in which memory, perceptual, and decision-making systems in the brain operate (Rolls, 2016). Humans can learn to apply logic, but it does not come naturally to the brain, and most humans are poor at logic. We are poor at any exact weighting of reward magnitude by probability to estimate utility. Thus we cannot assume in economics that humans always or even typically make logical or computationally accurate choices. We are poor at assessing the odds, and even weight possible wins and losses differently, for good biological reasons as I show below.

Humans do have an ability to reason using syntactical thought, even if it is not very frequently based on logic. Instead rational (reasoning) thought often uses heuristics, short-cut solutions that generally work, but may be more conservative, and certainly less precise, than would be computed by logic.

But the solution used by the brain may be less good for the individual than rational thought, because sometimes, and probabilistically caused by noise effects in the brain, the decision may be based not on rational thought, but instead on the goals of the gene-based emotional system which may not be in the interests of the individual, the phenome. Such choices may not be for the long-term benefit of the individual, but for the long-term benefit of the genes. What is good for the genome may not be good for the rational, self-interested, phenome (Rolls, 2014). Some examples follow.

## **7.2 Choices influenced by the gene-specified goals that may not be in the interests of the individual**

*Kin altruism.* People, and animals, are frequently altruistic towards those who are genetically related to them, and this is an example of the operation of ‘selfish genes’ (Dawkins, 1982, 1989; Dawkins, 1995; Ridley, 1996). But helping your genes may not help yourself. Mothers breast feed their children, sometimes at their own nutritional expense. The wish to pass on resources to their children, as inheritance, is highly valued by most people for biological reasons, that this is the best way to help their own genes, and this may not be realised consciously and rationally. Politicians should understand that this is of high value to most humans, and allow for this in their economic and financial proposals.

Tribalism has its origins in part in relation to kin altruism, and stakeholder altruism (see below). Although in modern times the local tribe (e.g. football crowd) may not be genetically related, identifying with members of the local group would in the past have led to helping individuals who would probably be genetically related, so that there would be a good chance that individuals would be helping their own genes. It is remarkable that until perhaps 80 years

ago most villagers in England would not travel more than a few villages away, and would probably find someone to love, marry, and have children with in that vicinity. This shows how the members of a local tribe would in the past probably have shared genes.

In relation to economics, the implication is that people may behave apparently altruistically to members of their ‘tribe’, and not behave strictly according to their own self-interest (Rolls, 2014). This may provide a contribution to understanding charitable behaviour: individuals in distant countries may, with the closeness to which they are brought by the media, be treated as members of one’s tribe, benefitting from this human heuristic. “For King and Country” is probably valued by individuals partly for the genetic advantage service might imply. Should it have been “For kin and country”? (The etymology of king is Anglo-Saxon kin.)

*Reciprocal altruism.* Altruism involves reciprocal exchange with an identified individual for the advantage of both. ‘Tit-for-tat’ can be stable, and forgiveness can be useful in economic games by re-establishing reciprocation when one and then the other party defect (Ridley, 1996). There are remarkably few well-established examples of reciprocal altruism involving individual recognition in animals: often proximity (clustering) (e.g. bats share blood with their neighbour, who happens to be in the same place regularly), and tribalism, or kin altruism provide an alternative account of what appears to be reciprocation (Dawkins, 1995). A cheat-proof label may help true reciprocal altruism. In humans, reciprocal altruism may become more important because there may be some language-based ‘contract’ between individuals between whom reciprocation is set up.

*Stakeholder altruism.* Being in a crowd may provide protection, even if one does not recognise an individual to whom to reciprocate. This is an example of stakeholder altruism. One might similarly have a stake in a country, or a wife. In all these cases, we can say that genes have identified genetic advantage in such altruism, even though it may not be to the individual’s advantage to participate fully. The individual might always for example find the middle of the crowd, and never take a duty on watch, and never be near the edge of the crowd where there is more danger; yet the genes for stakeholder altruism have to make it likely that individuals will participate in the giving as well as the receiving, and that cheats will be excluded (Roberts, 2005). Conforming to the decision-making of a group may be related to tribalism.

*Altruistic punishment.* In altruistic systems, cheat detection is important for the genetic, reciprocal, or stakeholder benefit. Individuals may therefore perform acts to their own apparent economic or other disadvantage, in order to punish or eliminate cheating, and this is termed altruistic punishment (Fehr, 2009).

There is an issue about whether altruistic punishment exists. Many of the experimental investigations into altruistic punishment do not make it clear enough that this is a single game, and that one will never encounter the individual again. If one may encounter the individual again, the punishment may not be so altruistic: it would then be self-interested, as it could be part of a reciprocal altruism interaction. Further, participants in some investigations may assume that at least the experimenter knows how they choose, and that could influence their behaviour.

*Reputation.* Reputation is important in reciprocal and stakeholder altruism. It leads to punishing, for example to exclusion, of individuals who gain a reputation for cheating or lying. Reputation is powerful, because one does not need to have directly experienced defection in reciprocation from an individual: knowledge that cheating, taking advantage, lying etc has occurred, being informed about it, can damage a person’s reputation, and influence interactions

with large numbers of individuals. Reputation is especially important in humans because of language, which can spread the rumour beyond those who have immediate contact with the individual. The media, newspapers, and the internet can be powerful communication tools for reputation: everyone is interested in their reputation, and in the reputation of others, because of the implications for them. A single rumour can be very damaging, so individuals may value highly anything to defend their reputation, even if it is very costly (in for example economic terms), risky, and may not succeed. An example is Oscar Wilde, who, valuing his reputation, took great risks in defending it, which led to great financial and other losses.

The importance of reputation is very high in humans because of language. The value of reputation to an individual must be taken into account when developing an understanding of the economic decisions made by individuals. Females value fidelity and trustworthiness as it is good for their genes to have the resources of their husband, and not to have those resources given to others. Women are thus very interested in reputation, and it has even been suggested that evolutionary pressure for the development of language was the value of gossip to women (Dunbar, 1996).

*Love, children, and parental economic and other sacrifice for children.* Love for one's partner with whom one is having children, and in one's children, is for a person's genetic advantage, but may not be for the individual's advantage (i.e. for the advantage of the phenotype). Some people devote themselves to science or art because of the value that discovery, creativity, or aesthetics has for them, or to business because of economic wealth, and do not have children, but this is not common, for reasons described above – the genetic advantage of reproduction must drive most people. These factors, rather than pure economic advancement of a self-interested individual, must be taken into account in understanding economic choices. Mothers have a built-in heuristic to help their children. Indeed, a need to be needed might be a good heuristic for a parent. And the heuristic might contribute to a number of other behaviours, such as helping the needy, unfortunate, and ill.

We have thus seen in this section that the self-interested financial advantage is often not the only factor that accounts for economic choices. Many other factors contribute, are built-in to us by genes that specify goals for actions, and may operate unconsciously, with confabulation sometimes not leading to an accurate account of why a choice was in fact made (Rolls, 2012a). We now turn to further neurobiological mechanisms that contribute to an account of economic choices and decision-making.

### ***Sexual selection***

Sexual selection can account for choices and decisions where the advantage may not be to the individual, to the individual's personal survival, to the phene, but instead is to the advantage of the individual's genes, by promoting reproductive success, enabling genes to be passed to the next generation (Miller, 2000; Rolls, 2012a, 2014, 2018). A classical example is the highly decorated nest built by the male bowerbird to attract females. The beautiful and elaborate nest may be a sign used by females to identify a male with good genes, one who can afford to invest in useless ornamentation. The obvious investment of time and resources may indicate a male who must be fit because it can survive the handicap of the large investment of time and resources. The aesthetic nest may also be a sign of a lot of brain power, which might of course also be useful in her offspring with him for other things, such as survival. The female

bowerbird, having chosen her male, and mated with him for his genes, then goes off to build a useful and practical nest in which to bring up the young. The male bowerbird's nest is thus as a nest just useless ornamentation; but it does attract females, and is therefore advantageous for sexual selection.

This is an example of *intersexual sexual selection*. It is probably at least part of the basis in humans of fashion, conspicuous consumption, thinness in females (a sign of sexual fertility, and of not being already pregnant), large breasts in females (frequently larger than necessary, but useful as a sign of child-rearing potential to males). Resources, wealth, and status in males are attractive to women, who may be able to bring up their children (genes) better with these advantages. Risk-taking may be attractive because if an individual can survive such risks, that individual must have good survival-related genes. Hunting ability may also be a sign of good genes: and made of value to individuals by inter-sexual selection.

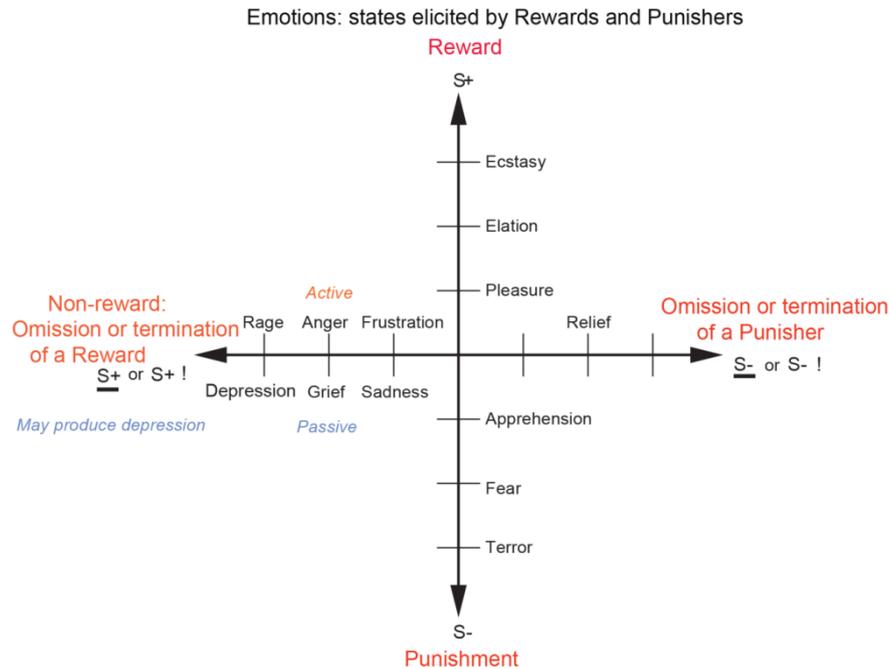
*Intrasexual sexual selection* involves competition between individuals of the same sex for access to the other sex. A large and fit body (or antlers in deer) are examples of weapons used in intrasexual selection. The tendency in males to aggression, fighting, and war may have foundations that are partly rooted in intrasexual selection.

We can thus see that neurobiology leads to the view that humans are not just self-interested individuals interested in financial wealth, but that there are many other factors, some of which may even harm the individual, that are important in economic choice. Evolutionary pressure has selected for brain systems that identify these as goals for choice and action, and economic choices should not therefore be assumed to be made only for the advantage of the self-interested individual. Humans may not even understand fully, or be able to explain and report correctly, the reasons for their choices, and this needs to be taken into account in economics. Moreover, the fact that choices are probabilistic, and are influenced by internal neuron spike timing-related noise, which even influences whether decisions are taken by the emotional or rational systems, needs to be taken into account in economics. Some foundations for understanding reward processing and decision-making have been described. A fuller approach to understanding reward processing and emotion is provided by Rolls (2014), a rigorous computational approach to understanding brain function is provided by Rolls (2016), neural decision-making is described by Rolls and Deco (2010) and Rolls (2014), and neuroeconomics is considered in Glimcher and Fehr (2013) with an introduction in Rolls (2014).

## **8      Commentary**

### ***What are emotions, and what types are there?***

I define emotions as states elicited by rewards and punishers. That is an operational definition, and helps greatly, for it means that emotions and their neural bases can be studied scientifically by investigating effects produced by rewards and punishers (Rolls, 1999a; Rolls, 2014). (The issue of conscious feelings is much more complex, and is considered elsewhere in Rolls (2014). Moreover, as summarized in Fig. 4, this approach leads to a classification of emotions in terms of reinforcement contingencies and each particular reward and punisher. (Examples are



*Figure 4:* Some of the emotional states associated with different reinforcement contingencies are indicated. Intensity increases away from the centre of the diagram, on a continuous scale. The classification scheme shows how different emotional states created by the different reinforcement contingencies consist of being in a state that leads to (1) performing an action to obtain a reward (S+), (2) performing an action to escape from or avoid a punisher (S-), (3) performing an action, or not, because of the omission of a reward (S+) (extinction) or the termination of a reward (S+!) (time out), and (4) performing an action, or not, because of the omission of a punisher (S-) (avoidance) or the termination of a punisher (S-!) (escape). Note that the vertical axis describes emotional states associated with the delivery of a reward (up) or punisher (down). The horizontal axis describes emotional states associated with the non-delivery of an expected reward (left) or the non-delivery of an expected punisher (right). For the contingency of non-reward (horizontal axis, left), different emotions can arise depending on whether an active action is possible to respond to the non-reward, or whether no action is possible, which is labelled as the passive condition. The diagram summarizes the emotional states that might arise for one reinforcer as a result of different contingencies. Every separate reinforcer has the potential to operate according to contingencies such as these. Each different reinforcer will produce different emotional states, but the contingencies will operate as shown to produce different specific emotional states for each different reinforcer. The diagram does not imply a dimensional theory of emotion, but shows the type of emotional state that might be produced by a specific reinforcer.

provided in Section 7.2, and the approach elaborated in detail elsewhere (Rolls, 2014).) This is much more systematic than trying to think of all the possible emotions that one can without having a framework (Ben-Ze'ev, 2001), even if the emotion 'types' are related to factor analysis (Barrett, 2017), electrical stimulation of the brain (Panksepp, 1998), facial expression (Ekman, 1992), etc (Solms, 2019).

In this framework, it needs to be emphasized that rewards and punishers can be 'primary', that is, gene-specified and innate (for example sweet taste), or 'secondary', that is learned by association with a primary reinforcer (Rolls, 1999a; Rolls, 2014). Thus money can be understood as a secondary reinforcer, because it has associations with many primary rewards.

***The relation of dual-systems brain theory, the emotional vs the rational, to behavioral macroeconomics***

A key point made in the paper is that Behavioral Macroeconomics may benefit from understanding the two very different types of computation performed in the brain to implement emotion vs rational thinking and rational decision-making. Many emotions involve actions to obtain goals (obtaining rewards and avoiding punishers) that are defined by genes, or are associated with those primary reinforcers. The computations involved are pattern association learning to learn stimulus-reward associations, and action-outcome learning (which is largely associative) to learn actions to obtain the goals of the actions, the outcome (Rolls, 2018, 2019b). Rational decision-making implies syntactical thought, which in humans is implemented in language, and also implies an ability to perform logic, and to help obtain an outcome that may be in the interests of the individual. The rationality principle in macroeconomics includes consistency in choices (Proto, 2019). The emotional system may thus be part of the basis for it not being safe to accept the rationality principle of economics, in that the emotional system may, often unconsciously, influence choices, and that may be exacerbated by noise in the decision-making system, as summarized in the present paper. Taking these factors into account may thus be important for behavioral macroeconomics, and that is one of the points made in this paper.

The issue of when the noise that influences decision-making in an individual averages out across a population of individuals is interesting. In neuronal networks the noise starts to average out as the number of nodes (neurons) in the system increases from 1,000 to 5,000 (Rolls and Deco, 2010; Deco et al., 2013; Rolls, 2016). However, macroeconomics may benefit from the understanding provided by these physics-related approaches in describing how the percentage of choices changes when the difference between the goods on offer varies. Behavioural macroeconomics needs to take into account this relationship, showing the way in which the average choice of many individuals changes as the values of the goods on offer changes. Behavioral macroeconomics may also need to take account of the fact that different individuals in a population will make different choices related to their personality, depending for example on the sensitivity of each individual to reward, to non-reward, to delayed reward as in delay discounting, etc (Glimcher and Fehr, 2013; Kahneman and Tversky, 2013; Rolls, 2014, 2018).

**Acknowledgements.** The author has worked on some of the experiments described here with I. Araujo, G.C. Baylis, L.L. Baylis, A. Bilderbeck, R. Bowtell, A.D. Browning, H.D. Critchley, S. Francis, F. Grabenhorst, M.E. Hasselmo, J. Hornak, M. Kadohisa, M. Kringelbach, C.M. Leonard, C. Margot, C. McCabe, F. McGlone, F. Mora, J. O'Doherty, B.A. Parris, D.I. Perrett, T.R. Scott, S.J. Thorpe, M.I. Velazco, J.V. Verhagen, E.A. Wakeman and F.A.W. Wilson, and their collaboration is sincerely acknowledged. Some of the research described was supported by the UK Medical Research Council.

<https://www.oxcns.org> Many of the papers referred to are available in .pdf form at this website, and so is a pdf of *Emotion and Decision-Making Explained* (Rolls, 2014).

## References

- Barrett, L.F. (2017). *How emotions are made: the secret life of the brain*. Houghton Mifflin Harcourt.
- Behrens, T.E., Woolrich, M.W., Walton, M.E., and Rushworth, M.F. (2007). Learning the value of information in an uncertain world. *Nature Neuroscience* 10:1214–1221. <https://www.nature.com/articles/nn1954>
- Ben-Ze'ev, A. (2001). *The subtlety of emotions*. MIT Press.
- Bernoulli, J. (1738 / 1954). Exposition of a new theory on the measurement of risk. *Econometrica* 22(1): 23–36. <https://www.jstor.org/stable/1909829>
- Booth, D.A. (1985). Food-conditioned eating preferences and aversions with interoceptive elements: learned appetites and satieties. *Ann N Y Acad Sci* 443: 22–37. <https://www.ncbi.nlm.nih.gov/pubmed/3860073>
- Cai, X., and Padoa-Schioppa, C. (2019). Neuronal evidence for good-based economic decisions under variable action costs. *Nature Communications* 10: article no. 393. <https://www.nature.com/articles/s41467-018-08209-3>
- Damasio, A.R. (1994). *Descartes' error*. New York: Putnam.
- Dawkins, M.S. (1995). *Unravelling animal behaviour*. Harlow: Longman.
- Dawkins, R. (1982). *The extended phenotype: the gene as the unit of selection*. San Francisco: W.H. Freeman.
- Dawkins, R. (1986). *The blind watchmaker*. Harlow: Longman.
- Dawkins, R. (1989). *The selfish gene, 2nd edition*. Oxford: Oxford University Press.
- de Araujo, I.E.T., Rolls, E.T., Velazco, M.I., Margot, C., and Cayeux, I. (2005). Cognitive modulation of olfactory processing. *Neuron* 46(4):671–679. <https://www.ncbi.nlm.nih.gov/pubmed/15944134>
- Deco, G., Rolls, E.T. (2005). Attention, short-term memory, and action selection: a unifying theory. *Progress in Neurobiology* 76(4):236–256. <https://www.sciencedirect.com/science/article/pii/S0301008205000912>
- Deco, G., Rolls, E.T. (2006). Decision-making and Weber's Law: a neurophysiological model. *Eur J Neurosci* 24(3): 901–916. <https://www.ncbi.nlm.nih.gov/pubmed/16930418>
- Deco, G., Rolls, E.T., and Romo, R (2009). Stochastic dynamics as a principle of brain function. *Progress in Neurobiology* 88(1):1–16. <https://www.sciencedirect.com/science/article/pii/S0301008209000197>
- Deco, G., Rolls, E.T., Albantakis, L., and Romo, R. (2013). Brain mechanisms for perceptual and reward-related decision-making. *Progress in Neurobiology* 103:194–213. <https://www.sciencedirect.com/science/article/pii/S0301008212000111>
- Dunbar, R. (1996). *Grooming, gossip, and the evolution of language*. London: Faber and Faber.
- Ekman, P. (1992). An argument for basic emotions. *Cognition and Emotion* 6(3–4):169–200. <https://www.tandfonline.com/doi/abs/10.1080/02699939208411068>

- Fehr, E. (2009). Social preferences and the brain. In Glimcher, P.W., Camerer, C.F., Fehr, E., and Poldrack, R.A. (eds.), *Neuroeconomics: decision-making and the brain*. London: Academic Press.
- Fouragnan, E., Retzler, C., and Philiastides, M.G. (2018). Separate neural representations of prediction error valence and surprise: Evidence from an fMRI meta-analysis. *Hum Brain Mapp* 39(7): 2887–2906. <https://www.ncbi.nlm.nih.gov/pubmed/29575249>
- Gilbert, S.J., and Burgess, P.W. (2008). Executive function. *Curr Biol* 18(3): R110–114.
- Gintis, H. (2000). *Game theory evolving*. Princeton: Princeton University Press.
- Glimcher, P. (2004). *Decisions, uncertainty, and the brain*. Cambridge, MA: MIT Press.
- Glimcher, P.W. (2011). *Foundations of neuroeconomic analysis*. Oxford: Oxford University Press.
- Glimcher, P.W., and Fehr, E., eds. (2013). *Neuroeconomics: decision-making and the brain, 2nd edition*. New York: Academic Press.
- Goldman-Rakic, P.S. (1996). The prefrontal landscape: implications of functional architecture for understanding human mentation and the central executive. *Philosophical Transactions of the Royal Society B* 351:1445–1453. <https://www.ncbi.nlm.nih.gov/pubmed/8941956>
- Grabenhorst, F., and Rolls E.T. (2008). Selective attention to affective value alters how the brain processes taste stimuli. *Eur J Neurosci* 27(3): 723–729. <https://www.ncbi.nlm.nih.gov/pubmed/18279324>
- Grabenhorst, F., and Rolls, E.T. (2009). Different representations of relative and absolute value in the human brain. *Neuroimage* 48(1): 258–268. <https://www.ncbi.nlm.nih.gov/pubmed/19560545>
- Grabenhorst, F., and Rolls E.T. (2010). Attentional modulation of affective vs sensory processing: functional connectivity and a top-down biased activation theory of selective attention. *J Neurophysiol* 104:1649–1660.
- Grabenhorst, F., and Rolls, E.T. (2011) Value, pleasure, and choice in the ventral prefrontal cortex. *Trends Cogn Sci* 15(2): 56–67. <https://www.ncbi.nlm.nih.gov/pubmed/21216655>
- Grabenhorst, F., Rolls, E.T., and Bilderbeck, A. (2008a). How cognition modulates affective responses to taste and flavor: top down influences on the orbitofrontal and pregenual cingulate cortices. *Cereb Cortex* 18(7): 1549–1559. <https://www.ncbi.nlm.nih.gov/pubmed/18056086>
- Grabenhorst, F., Rolls, E.T., and Parris, B.A. (2008b). From affective value to decision-making in the prefrontal cortex. *Eur J Neurosci* 28(9): 1930–1939. <https://www.ncbi.nlm.nih.gov/pubmed/18973606>
- Hamilton, W.D. (1964). The genetical evolution of social behaviour. *Journal of Theoretical Biology* 7(1):1–16. <https://www.sciencedirect.com/science/article/pii/0022519364900384>
- Hamilton, W.D. (1996). *Narrow roads of gene land*. New York: W.H. Freeman.
- Hasselmo, M.E., Rolls, E.T., and Baylis, G.C. (1989). The role of expression and identity in the face-selective responses of neurons in the temporal visual cortex of the monkey. *Behavioural Brain Research* 32(3): 203–218. <https://www.sciencedirect.com/science/article/pii/S0166432889800543>
- Hebb, D.O. (1949). *The organization of behavior: a neuropsychological theory*. New York: Wiley.

- Heekeren, H.R., Wartenburger, I., Schmidt H., Prehn, K., Schwintowski, H.P., and Villringer, A. (2005). Influence of bodily harm on neural correlates of semantic and moral decision-making. *Neuroimage* 24(3): 887–897. <https://www.ncbi.nlm.nih.gov/pubmed/15652323>
- Hornak, J., O'Doherty, J., Bramham, J., Rolls, E.T., Morris, R.G., Bullock, P.R., and Polkey, C.E. (2004). Reward-related reversal learning after surgical excisions in orbitofrontal and dorsolateral prefrontal cortex in humans. *J Cogn Neurosci* 16(3): 463–478. <https://www.ncbi.nlm.nih.gov/pubmed/15072681>
- Insabato, A., Pannunzi, M., Rolls, E.T., and Deco, G. (2010). Confidence-related decision-making. *J Neurophysiol* 104(1):539–547. <https://www.ncbi.nlm.nih.gov/pubmed/20393062>
- Izuma, K., Saito, D.N., and Sadato, N. (2008). Processing of social and monetary rewards in the human striatum. *Neuron* 58(2): 284–294. <https://www.sciencedirect.com/science/article/pii/S0896627308002663>
- Kable, J.W., and Glimcher, P.W. (2007). The neural correlates of subjective value during intertemporal choice. *Nat Neurosci* 10(12):1625–1633. <https://www.ncbi.nlm.nih.gov/pubmed/17982449>
- Kahneman, D., and Tversky, A. (1979). Prospect theory: An analysis of decision under risk. *Econometrica* 47(2): 263–292. <https://www.jstor.org/stable/1914185>
- Kahneman, D., and Tversky, A. (1984). Choices, values, and frames. *American Psychologist* 39(4):341–350. <https://psycnet.apa.org/record/1985-05780-001>
- Kahneman, D., and Tversky, A. (2013). Choices, values, and frames. In MacLean, L.C. and Ziemba, W.T., *Handbook of the fundamentals of financial decision making: Part I*. World Scientific.
- Kolb, B., and Whishaw, I.Q. (2015). *Fundamentals of human neuropsychology, 7th edition*. New York: Worth.
- Krebs, J.R., and Kacelnik, A. (1991). Decision making. In Krebs, J.R. and Davies, N.B. (eds.), *Behavioural ecology, 3rd edition*. Oxford: Blackwell.
- Kringelbach, M.L., and Rolls, E.T. (2003). Neural correlates of rapid reversal learning in a simple model of human social interaction. *Neuroimage* 20(3):1371–1383. <https://www.ncbi.nlm.nih.gov/pubmed/14568506>
- Maia, T.V., and McClelland, J.L. (2004). A reexamination of the evidence for the somatic marker hypothesis: what participants really know in the Iowa gambling task. *Proc Natl Acad Sci USA* 101(45): 16075–16080. <https://www.ncbi.nlm.nih.gov/pubmed/15501919>
- Marsh, A.A., Blair, K.S., Vythilingam, M., Busis, S., and Blair, R.J. (2007). Response options and expectations of reward in decision-making: the differential roles of dorsal and rostral anterior cingulate cortex. *Neuroimage* 35(2): 979–988. <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC1868682/>
- McCabe, C., Rolls, E.T., Bilderbeck, A., and McGlone, F. (2008). Cognitive influences on the affective representation of touch and the sight of touch in the human brain. *Social Cognitive and Affective Neuroscience* 3(2): 97–108. <https://psycnet.apa.org/record/2008-07515-003>
- McClure, S.M., Laibson, D.I., Loewenstein, G., and Cohen, J.D. (2004). Separate neural systems value immediate and delayed monetary rewards. *Science* 306(5695): 503–507. <https://science.sciencemag.org/content/306/5695/503>

- McFarland, D.J. (1989). *Problems of animal behaviour*. Harlow: Longman.
- Miller, G.F. (2000). *The mating mind*. London: Heinemann.
- Mobbs, D., Trimmer, P.C., Blumstein, D.T., and Dayan, P. (2018). Foraging for foundations in decision neuroscience: insights from ethology. *Nature Reviews Neuroscience* 19: 419–427.  
<https://www.nature.com/articles/s41583-018-0010-7>
- Montague, P.R., and Berns, G.S. (2002). Neural economics and the biological substrates of valuation. *Neuron* 36(2): 265–284. <https://www.sciencedirect.com/science/article/pii/S0896627302009741>
- O'Doherty, J., Kringelbach, M.L., Rolls, E.T., Hornak, J., and Andrews, C. (2001). Abstract reward and punishment representations in the human orbitofrontal cortex. *Nat Neurosci* 4(1): 95–102.  
<https://www.ncbi.nlm.nih.gov/pubmed/11135651>
- Padoa-Schioppa, C., and Assad, J.A. (2006). Neurons in the orbitofrontal cortex encode economic value. *Nature* 441: 223–226. <https://www.nature.com/articles/nature04676>
- Padoa-Schioppa, C., and Assad, J.A. (2008). The representation of economic value in the orbitofrontal cortex is invariant for changes of menu. *Nature Neuroscience* 11: 95–102.  
<https://www.nature.com/articles/nn2020>
- Padoa-Schioppa, C., and Conen, K.E. (2017). Orbitofrontal cortex: a neural circuit for economic decisions. *Neuron* 96(4): 736–754. <https://www.ncbi.nlm.nih.gov/pubmed/29144973>
- Panksepp, J. (1998). *Affective neuroscience: the foundations of human and animal emotions*. New York: Oxford University Press.
- Proto, E. (2019). Report of the paper Emotion and reasoning in human decision-making. Open-peer-review report (July 22, 2019) on Edmund T. Rolls (2019). Emotion and reasoning in human decision-making. Economics Discussion Papers, No 2019-8.  
<http://www.economics-ejournal.org/economics/discussionpapers/2019-8#anchor.comment.2019-07-22.8348814495>
- Rangel, A., Camerer, C., and Montague, P.R. (2008). A framework for studying the neurobiology of value-based decision making. *Nature Reviews Neuroscience* 9: 545–556.  
<https://www.nature.com/articles/nrn2357>
- Ridley, M. (1993). *The red queen: sex and the evolution of human nature*. London: Penguin.
- Ridley, M. (1996). *The origins of virtue*. London: Viking.
- Roberts, G. (2005). Cooperation through interdependence. *Animal Behaviour* 70(4): 901–908.  
<https://www.sciencedirect.com/science/article/pii/S0003347205002216>
- Rolls, E.T. (1999a). *The brain and emotion*. Oxford: Oxford University Press.
- Rolls, E.T. (1999b). The functions of the orbitofrontal cortex. *Neurocase* 5(4): 301–312.  
<https://www.tandfonline.com/doi/abs/10.1080/13554799908411984>
- Rolls, E.T. (2000). Functions of the primate temporal lobe cortical visual areas in invariant visual object and face recognition. *Neuron* 27(2):205–218. <https://www.ncbi.nlm.nih.gov/pubmed/10985342>
- Rolls, E.T. (2007). A computational neuroscience approach to consciousness. *Neural Networks* 20(9): 962–982. <https://www.sciencedirect.com/science/article/pii/S089360800700189X>

- Rolls, E.T. (2009a). The anterior and midcingulate cortices and reward. In Vogt, B.A. (ed.), *Cingulate neurobiology and disease*. Oxford: Oxford University Press.
- Rolls, E.T. (2009b). From reward value to decision-making: neuronal and computational principles. In Dreher, J.-C., and Tremblay, L. (eds.), *Handbook of reward and decision-making*. New York: Academic Press.
- Rolls, E.T. (2011) Consciousness, decision-making, and neural computation. In Cutsuridis, V., Hussain, A., and Taylor, J.G. (eds.), *Perception-action cycle: models, algorithms and systems*. Berlin: Springer.
- Rolls, E.T. (2012a). *Neuroculture. On the implications of brain science*. Oxford: Oxford University Press.
- Rolls, E.T. (2012b). Invariant visual object and face recognition: neural and computational bases, and a model, VisNet. *Front Comput Neurosci* 6(35):1–70.  
<https://www.ncbi.nlm.nih.gov/pubmed/22723777>
- Rolls, E.T. (2014). *Emotion and decision-making explained*. Oxford: Oxford University Press. Available for download at [www.oxcns.org](http://www.oxcns.org).
- Rolls, E.T. (2016). *Cerebral cortex: principles of operation*. Oxford: Oxford University Press.
- Rolls, E.T. (2017). The roles of the orbitofrontal cortex via the habenula in non-reward and depression, and in the responses of serotonin and dopamine neurons. *Neurosci Biobehav Rev* 75: 331–334.  
<https://www.ncbi.nlm.nih.gov/pubmed/28223097>
- Rolls, E.T. (2018). *The brain, emotion, and depression*. Oxford: Oxford University Press.
- Rolls, E.T. (2019a). The orbitofrontal cortex and emotion in health and disease, including depression. *Neuropsychologia* 128: 14–43. <https://www.ncbi.nlm.nih.gov/pubmed/28951164>
- Rolls, E.T. (2019b). The cingulate cortex and limbic systems for emotion, action, and memory. *Brain Structure and Function*: <https://link.springer.com/article/10.1007/s00429-019-01945-2>
- Rolls, E.T. (2019c). *The orbitofrontal cortex*. Oxford: Oxford University Press.
- Rolls, E.T., and Baylis, L.L. (1994). Gustatory, olfactory, and visual convergence within the primate orbitofrontal cortex. *J Neurosci* 14(9): 5437–5452.
- Rolls, E.T., and Treves, A. (1998). *Neural networks and brain function*. Oxford: Oxford University Press.
- Rolls, E.T., and Grabenhorst, F. (2008). The orbitofrontal cortex and beyond: from affect to decision-making. *Progress in Neurobiology* 86(3): 216–244.  
<https://www.sciencedirect.com/science/article/pii/S0301008208000981>
- Rolls, E.T., and Deco, G. (2010). *The noisy brain: stochastic dynamics as a principle of brain function*. Oxford: Oxford University Press.
- Rolls, E.T., Judge, S.J., and Sanghera, M. (1977). Activity of neurones in the inferotemporal cortex of the alert monkey. *Brain Research* 130(2): 229–238.  
<https://www.sciencedirect.com/science/article/pii/0006899377902724>
- Rolls, E.T., McCabe, C., and Redoute, J. (2008a). Expected value, reward outcome, and temporal difference error representations in a probabilistic decision task. *Cereb Cortex* 18(3): 652–663.  
<https://www.ncbi.nlm.nih.gov/pubmed/17586603>

- Rolls, E.T., Grabenhorst, F., and Deco, G. (2010a). Decision-making, errors, and confidence in the brain. *J Neurophysiol* 104(5): 2359–2374. <https://www.ncbi.nlm.nih.gov/pubmed/20810685>
- Rolls, E.T., Grabenhorst, F., and Parris, B.A. (2010b). Neural systems underlying decisions about affective odors. *J Cogn Neurosci* 22(5): 1069–1082. <https://www.ncbi.nlm.nih.gov/pubmed/19320548>
- Rolls, E.T., Grabenhorst, F., and Deco, G. (2010c). Choice, difficulty, and confidence in the brain. *Neuroimage* 53(2): 694–706. <https://www.ncbi.nlm.nih.gov/pubmed/20615471>
- Rolls, E.T., Hornak, J., Wade, D., and McGrath, J. (1994). Emotion-related learning in patients with social and emotional changes associated with frontal lobe damage. *J Neurol Neurosurg Psychiatry* 57(12): 1518–1524. <https://www.ncbi.nlm.nih.gov/pubmed/7798983>
- Rolls, E.T., Critchley, H.D., Mason, R., and Wakeman, E.A. (1996). Orbitofrontal cortex neurons: role in olfactory and visual association learning. *J Neurophysiol* 75(5): 1970–1981. <https://www.ncbi.nlm.nih.gov/pubmed/8734596>
- Rolls, E.T., Critchley, H.D., Browning, A.S., and Inoue, K. (2006). Face-selective and auditory neurons in the primate orbitofrontal cortex. *Exp Brain Res* 170(1): 74–87. <https://www.ncbi.nlm.nih.gov/pubmed/16328289>
- Rolls, E.T., Grabenhorst, F., Margot C., da Silva, M.A.A.P., and Velazco, M.I. (2008b). Selective attention to affective value alters how the brain processes olfactory stimuli. *J Cogn Neurosci* 20(10): 1815–1826. <https://www.ncbi.nlm.nih.gov/pubmed/18370603>
- Rushworth, M.F., Kolling, N., Sallet, J., and Mars, R.B. (2012). Valuation and decision-making in frontal cortex: one or many serial or parallel systems? *Curr Opin Neurobiol* 22(6): 946–955. <https://www.ncbi.nlm.nih.gov/pubmed/22572389>
- Schultz, W. (2016). Dopamine reward prediction-error signalling: a two-component response. *Nat Rev Neurosci* 17(3): 183–195. <https://www.ncbi.nlm.nih.gov/pubmed/26865020>
- Sescousse, G., Li, Y., and Dreher, J.C. (2015). A common currency for the computation of motivational values in the human striatum. *Soc Cogn Affect Neurosci* 10(4): 467–473. <https://www.ncbi.nlm.nih.gov/pubmed/24837478>
- Shallice, T., and Cipolotti, L. (2018). The prefrontal cortex and neurological impairments of active thought. *Annu Rev Psychol* 69: 157–180. <https://www.ncbi.nlm.nih.gov/pubmed/28813204>
- Solms, M. (2019). Commentary on Edmund Rolls: ‘Emotion and reason in human decision-making’. Economics Discussion Papers, No 2019-45, Kiel Institute for the World Economy. <http://www.economics-ejournal.org/economics/discussionpapers/2019-45>
- Sutton, R.S., and Barto, A.G. (1998). *Reinforcement learning*. Cambridge, MA: MIT Press.
- Thorpe, S.J., Rolls, E.T., and Maddison, S. (1983). Neuronal activity in the orbitofrontal cortex of the behaving monkey. *Exp Brain Res* 49(1): 93–115. <https://www.ncbi.nlm.nih.gov/pubmed/6861938>
- Tremblay, L., and Schultz, W. (1999). Relative reward preference in primate orbitofrontal cortex. *Nature* 398: 704–708. <https://www.nature.com/articles/19525>
- Tversky, A., and Kahneman, D. (1986). Rational choice and the framing of decisions. *Journal of Business* 59(4): 251–278. <https://www.jstor.org/stable/2352759>

von Neumann, J., and Morgenstern, O. (1944). *The theory of games and economic behavior*. Princeton: Princeton University Press.

Wang, X.J. (2002). Probabilistic decision making by slow reverberation in cortical circuits. *Neuron* 36(5): 955–968. [https://doi.org/10.1016/S0896-6273\(02\)01092-9](https://doi.org/10.1016/S0896-6273(02)01092-9)

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