

Value, pleasure and choice in the ventral prefrontal cortex

Fabian Grabenhorst¹ and Edmund T. Rolls²

¹ University of Cambridge, Department of Physiology, Development and Neuroscience, Cambridge, UK

² Oxford Centre for Computational Neuroscience, Oxford, UK

Rapid advances have recently been made in understanding how value-based decision-making processes are implemented in the brain. We integrate neuroeconomic and computational approaches with evidence on the neural correlates of value and experienced pleasure to describe how systems for valuation and decision-making are organized in the prefrontal cortex of humans and other primates. We show that the orbitofrontal and ventromedial prefrontal (VMPFC) cortices compute expected value, reward outcome and experienced pleasure for different stimuli on a common value scale. Attractor networks in VMPFC area 10 then implement categorical decision processes that transform value signals into a choice between the values, thereby guiding action. This synthesis of findings across fields provides a unifying perspective for the study of decision-making processes in the brain.

Integrating different approaches to valuation and decision-making

Consider a situation where a choice has to be made between consuming an attractive food and seeking a source of warm, pleasant touch. To decide between these fundamentally different rewards, the brain needs to compute the values and costs associated with two multisensory stimuli, integrate this information with motivational, cognitive and contextual variables and then use these signals as inputs for a stimulus-based choice process. Rapid advances have been made in understanding how these key component processes for value-based, economic decision-making are implemented in the brain. Here, we review recent findings from functional neuroimaging, single neuron recordings and computational neuroscience to describe how systems for stimulus-based (goal-based) valuation and choice decision-making are organized and operate in the primate, including human, prefrontal cortex.

When considering the neural basis of value-based decision-making, the sensory nature of rewards is often neglected, and the focus is on action-based valuation and choice. However, many choices are between different sensory and, indeed, multisensory rewards, and can be action independent [1–3]. Here, we bring together evidence from investigations of the neural correlates of the experienced pleasure produced by sensory rewards and from studies that have used neuroeconomic and computational approaches,

thereby linking different strands of research that have largely been considered separately so far.

Neural systems for reward value and its subjective correlate, pleasure

Reward and emotion: a Darwinian perspective

The valuation of rewards is a key component process of decision-making. The neurobiological and evolutionary context is as follows [3]. Primary rewards, such as sweet taste and warm touch, are gene-specified (i.e. unlearned) goals for action built into us during evolution by natural selection to direct behavior to stimuli that are important for survival and reproduction. Specification of rewards, the goals for action, by selfish genes is an efficient and adaptive Darwinian way for genes to control behavior for their own reproductive success [3]. Emotions are states elicited when these gene-specified rewards are received, omitted, or terminated, and by other stimuli that become linked with them by associative learning [3]. The same approach leads to understanding motivations or ‘wantings’ as states in which one of these goals is being sought [3]. (This approach suggests that when animals perform responses for rewards that have been devalued, which have been described as ‘wantings’ [4], such behavior is habit or stimulus-response based after over-training, and is not goal directed.) Neuronal recordings in macaques, used as a model for these systems in humans [3], and functional neuroimaging studies in humans have led to the concept of three tiers of cortical processing [1], illustrated in Figure 1 and described in this review.

Object representations independent of reward valuation: Tier 1

The first processing stage is for the representation of what object or stimulus is present, independently of its reward value and subjective pleasantness. In this first tier, the identity and intensity of stimuli are represented, as exemplified by correlations of activations in imaging studies with the subjective intensity but not pleasantness of taste in the primary taste cortex [5,6], and neuronal activity that is independent of reward value, investigated, for example, when food value is reduced to zero by feeding to satiety [1,3]. As shown in Figure 1, this first tier includes the primary taste cortex in the anterior insula, the pyriform olfactory cortex and the inferior temporal visual cortex, where objects and faces are represented relatively invariantly with respect to position on the retina, size, view and so on, where this invariant representation is ideal for association with a reward [1,3,7]. Part of the utility of a ‘what’ representation

Corresponding authors: Rolls, E.T. (Edmund.Rolls@oxcns.org).
URL: www.oxcns.org

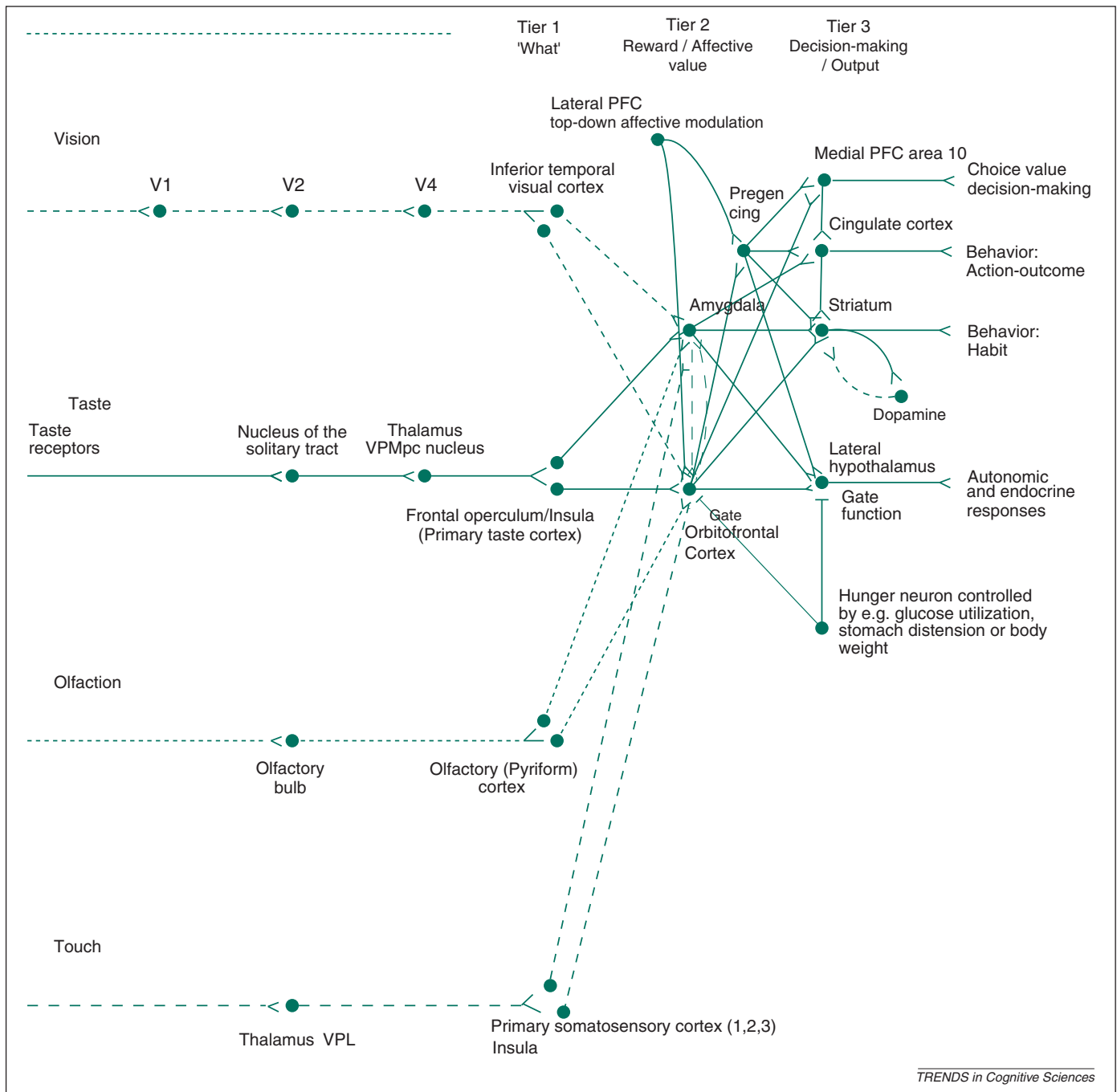


Figure 1. Organization of cortical processing for computing value (in Tier 2) and making value-based decisions (in Tier 3) and interfacing to action systems. The Tier 1 brain regions up to and including the column headed by the inferior temporal visual cortex compute and represent neuronally 'what' stimulus or object is present, but not its reward or affective value. Tier 2 represents, by its neuronal firing, the reward or affective value, and includes the OFC, amygdala, and anterior including pregenual cingulate cortex. Tier 3 is involved in choices based on reward value (in particular VMPFC area 10), and in different types of output to behavior. The secondary taste cortex and the secondary olfactory cortex are within the orbitofrontal cortex. Abbreviations: lateral PFC, lateral prefrontal cortex, a source for top-down attentional and cognitive modulation of affective value [50]; PreGen Cing, pregenual cingulate cortex; V1, primary visual cortex; V4, visual cortical area V4. 'Gate' refers to the finding that inputs such as the taste, smell and sight of food in regions where reward value is represented only produce effects when an appetite for the stimulus (modulated e.g. by hunger) is present [3]. Adapted, with permission, from [1].

independent of reward value is that one can learn about an object, for example about its location and properties, even when it is not rewarding, for example when satiated.

Reward value and pleasure: Tier 2

The orbitofrontal cortex: the value and pleasure of stimuli
Receiving inputs from Tier 1, the primate, including human, orbitofrontal cortex (OFC) in Tier 2 (Figure 1) is the first stage of cortical processing in which reward value is made explicit in the representation. This is supported by

discoveries that: (i) OFC neurons decrease their responses to a food or to water to zero when the reward values of food and water are reduced to zero by feeding to satiety; (ii) OFC neurons with visual responses learn rapidly and reverse their responses to visual stimuli depending on whether the stimulus is associated with a reward or punisher; and (iii) activations in humans are related to the reward value of taste, olfactory, oral texture, somatosensory, visual, social and monetary stimuli [1,3] (Table 1 and the supplementary material online for references). Subjective pleasure is the

Table 1. Principles of operation of the OFC and ACC in reward processing, and their adaptive value^a

Operational principle	Adaptive value
1. Neural activity in the OFC and ACC represents reward value and pleasure on a continuous scale.	This type of representation provides useful inputs for neural attractor networks involved in choice decision-making.
2. The identity and intensity of stimuli are represented at earlier cortical stages that send inputs to the OFC and ACC: stimuli and objects are first represented, then their reward and affective value is computed in the OFC.	This separation of sensory from affective processing is highly adaptive for it enables one to identify and learn about stimuli independently of whether one currently wants them and finds them rewarding.
3. Many different rewards are represented close together in the OFC, including taste, olfactory, oral texture, temperature, touch, visual, social, amphetamine-induced and monetary rewards.	This organization facilitates comparison and common scaling of different rewards by lateral inhibition, and thus provides appropriately scaled inputs for a choice decision-making process.
4. Spatially separate representations of pleasant stimuli (rewards) and unpleasant stimuli (punishers) exist in the OFC and ACC.	This type of organization provides separate and partly independent inputs into brain systems for cost-benefit analysis and decision-making.
5. The value of specific rewards is represented in the OFC: different single neurons respond to different combinations of specific taste, olfactory, fat texture, oral viscosity, visual, and face and vocal expression rewards.	This type of encoding provides a reward window on the world that allows not only selection of specific rewards, but also for sensory-specific satiety, a specific reduction in the value of a stimulus after it has been received continuously for a period of time.
6. Both absolute and relative value signals are present in the OFC.	Absolute value is necessary for stable long-term preferences and transitivity. Being sensitive to relative value might be useful in climbing local reward gradients as in positive contrast effects.
7. Top-down cognitive and attentional factors, originating in lateral prefrontal cortex, modulate reward value and pleasantness in the OFC and ACC through biased competition and biased activation.	These top-down effects allow cognition and attention to modulate the first cortical stage of reward processing to influence valuation and economic decision-making.

^aReferences to the investigations that provide the evidence for this summary are provided in the [supplementary material online](#).

consciously experienced affective state produced by rewarding stimuli [3]. In imaging studies, neural activations in the OFC and adjacent anterior cingulate cortex (ACC) are correlated with the subjective pleasure produced by many different stimuli (Figure 2a). For example, the subjective pleasantness of the oral texture of fat, an indicator for high energy density in foods, is represented on a continuous scale by neural activity in the OFC and ACC (Figure 2b) [8].

Neuroeconomic approaches focus largely on subjective value as inferred from choices (revealed preferences). By contrast, pleasure is a consciously experienced state. The conscious route to choice and action may be needed for rational (i.e. reasoning) thought about multistep plans [3,9]. Primary rewards would become conscious by virtue of entering a reasoning processing system, for example when reasoning about whether an experienced reward, such as a pleasant touch, should be sought in future [3,9,10]. Because pleasure may reflect processing by a reasoning, conscious system when decision-making is performed by goal-directed explicit decision systems involving the prefrontal cortex (as opposed to implicit habit systems involving the basal ganglia) [1,3,11], pleasure may provide insight into what guides decision-making beyond what can be inferred from observed choices [12].

The ACC: the reward value of stimuli; and an interface to goal-directed action The pleasure map in Figure 2 indicates that the ACC, which receives inputs from the OFC (Figure 1), also has value-based representations, consistent with evidence from single neuron studies [13–17]. These value representations provide the goal representation in an ‘action to goal outcome’ associative learning system in the mid-cingulate cortex (Box 1), and also provide an output for autonomic responses to affective stimuli [18].

Key principles of value representations in the OFC and ACC

Key principles of operation of the OFC and ACC in reward and punishment valuation are summarized in Table 1. We examine some of these principles, focusing on recent developments in understanding how valuation signals in the OFC and ACC are scaled, how they adapt to contexts and how they are modulated by top-down processes.

Box 1. Reward representations in the ACC

If activations in both the OFC and ACC reflect the value of rewards, what might be the difference in function between these two areas [1,18,89]? We suggest that the information about the value of rewards is projected from the OFC to ACC (its pregenual and dorsal anterior parts). The pregenual and dorsal ACC parts can be conceptualized as a relay that allows information about rewards and outcomes to be linked, via longitudinal connections running in the cingulum fiber bundle, to information about actions represented in the mid-cingulate cortex.

Bringing together information about specific rewards with information about actions, and the costs associated with actions, is important for associating actions with the value of their outcomes and for selecting the correct action that will lead to a desired reward [89,90]. Indeed, consistent with its strong connections to motor areas [91], lesions of ACC impair reward-guided action selection [92,93], neuroimaging studies have shown that the ACC is active when outcome information guides choices [94], and single neurons in the ACC encode information about both actions and outcomes, including reward prediction errors for actions [14,15]. For example, Luk and Wallis [14] found that, in a task where information about three potential outcomes (three types of juice) had to be associated on a trial-by-trial basis with two different responses (two lever movements), many neurons in the ACC encoded information about both specific outcomes and specific actions. In a different study, Seo and Lee [17] found that dorsal ACC neurons encoded a signal related to the history of rewards received in previous trials, consistent with a role for this region in learning the value of actions. Interestingly, in both of these studies, there was little evidence for encoding of choices, indicating that a choice mechanism between rewards might not be implemented in the ACC.

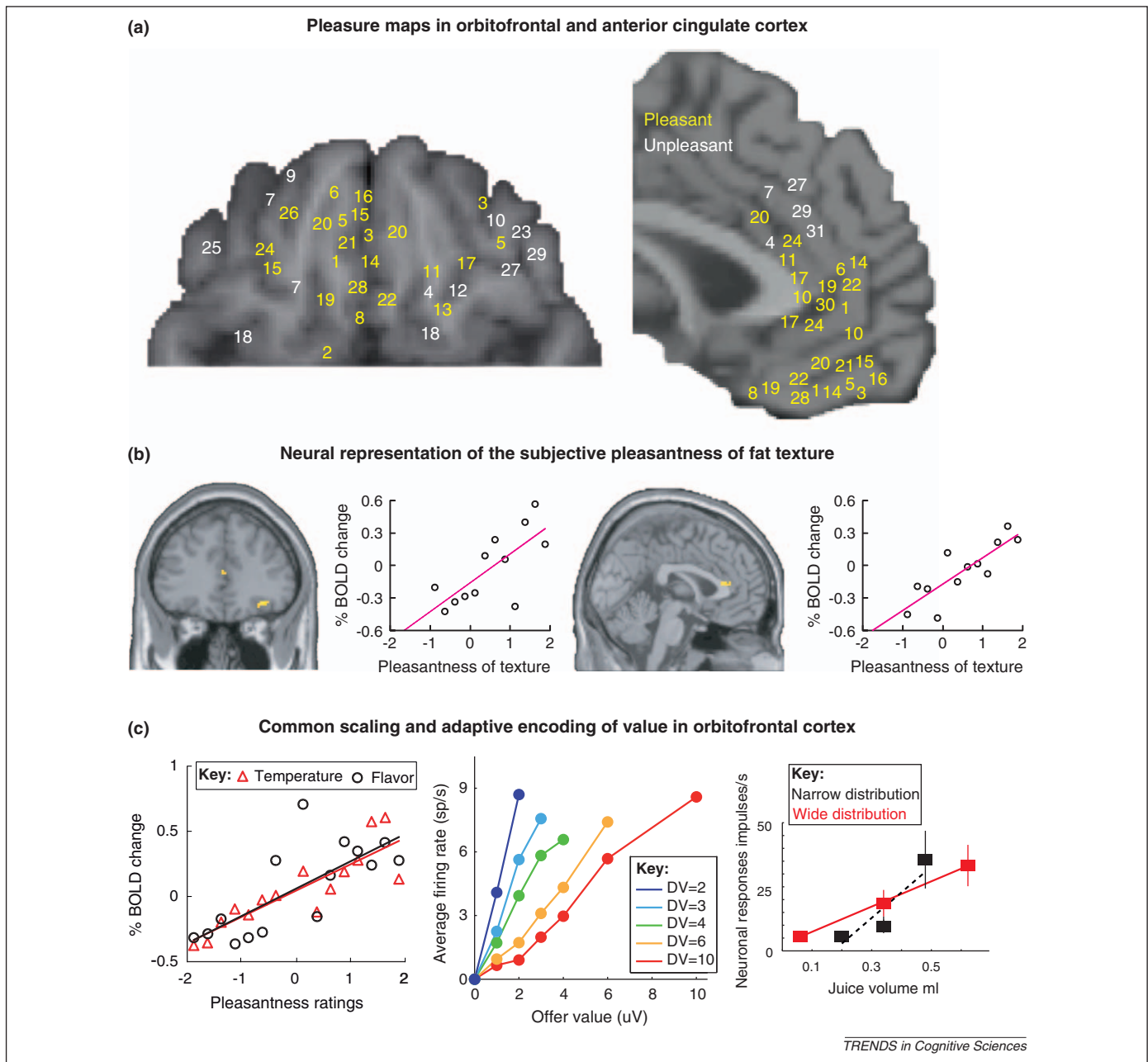


Figure 2. Pleasure and value in the brain. **(a)** Maps of subjective pleasure in the OFC (ventral view) and ACC (sagittal view). Yellow font indicates sites where activations correlate with subjective pleasantness; whereas white font indicates sites where activations correlate with subjective unpleasantness. The numbers refer to effects found in specific studies: taste: 1, 2; odor: 3–10; flavor: 11–16; oral texture: 17, 18; chocolate: 19; water: 20; wine: 21; oral temperature: 22, 23; somatosensory temperature: 24, 25; the sight of touch: 26, 27; facial attractiveness: 28, 29; erotic pictures: 30; and laser-induced pain: 31. (See the supplementary material online for references to the original studies.) **(b)** How the brain represents the reward value of the oral texture (i.e. the mouth feel) of food stimuli [8]. Oral texture is a prototypical primary reward important for detecting the presence of fat in foods and is thus an indicator of high energy density in foods. Subjective pleasantness (+2 = very pleasant, -2 = very unpleasant) of the oral texture of liquid food stimuli that differed in flavor and fat content tracked neural activity (% BOLD signal change) in the OFC (left) and ACC (right). **(c)** Common scaling and adaptive encoding of value in the OFC. (left) A common scale for the subjective pleasure for different primary rewards: neural activity in the OFC correlates with the subjective pleasantness ratings for flavor stimuli in the mouth and somatosensory temperature stimuli delivered to the hand. The regression lines describing the relationship between neural activity (% BOLD signal) and subjective pleasantness ratings were indistinguishable for both types of reward. (middle) Padoa-Schioppa [43] found that neurons in the OFC that encode the offer value of different types of juice adapt their sensitivity to the value range of juice rewards available in a given session, while keeping their neuronal activity range constant. Each line shows the average neuronal response for a given value range. (right) Kobayashi *et al.* [44] found that neurons in the OFC adapt their sensitivity of value coding to the statistical distribution of reward values, in that the reward sensitivity slope adapted to the standard deviation of the probability distribution of juice volumes. These findings indicate that the range of the value scale in the OFC can be adjusted to reflect the range of rewards that are available at a given time. Reproduced, with permission, from [30] (c left), [43] (c middle) and [44] (c right).

Reward-specific value representations on a common scale, but not in a common currency

Reward-specific representations Single neurons in the OFC encode different specific rewards [1,3] by responding to different combinations of taste, olfactory, somatosensory, visual and auditory stimuli, including socially relevant

stimuli such as face expression [1,3,19]. Part of the adaptive utility of this reward-specific representation is that it provides for sensory-specific satiety as implemented by a decrease in the responsiveness of reward-specific neurons [1]. This is a fundamental property of every reward system that helps to ensure that a variety of

different rewards is selected over time [3]. Representations of both reward outcome and expected value are specific for the particular reward: not only do different neurons respond to different primary reinforcers, but different neurons also encode the conditioned stimuli for different outcomes, with different neurons responding, for example, to the sight or odor of stimuli based on the outcome that is expected [20,21].

Topology of reward and punishment systems Different types of reward tend to be represented in the human medial OFC and pregenual ACC, and different types of punisher tend to be represented in the lateral OFC and the dorsal part of the ACC (Figure 2). The punishers include negative reward prediction error encoded by neurons that fire only when an expected reward is not received [20]. To compute this OFC signal, inputs are required from neurons that respond to the expected value of a stimulus (exemplified in the OFC by neurons that respond to the sight of food), and from other neurons that respond to the magnitude of the reward outcome (exemplified in the OFC by neurons that respond to the taste of food) [3,22]. All these signals are reflected in activations found for expected value and for reward outcome in the human medial OFC [23,24], and for monetary loss and negative reward prediction error for social reinforcers in the human lateral OFC [25]. This topological organization with different types of specific reward represented close together in the OFC may allow for comparison between different rewards implemented by lateral inhibition as part of a process of scaling different specific rewards to the same range [3]. A topological organization of reward and punishment systems is also important to provide partly separate inputs into systems for learning, choice and cost-benefit analysis (Box 2).

A common scale for different specific rewards A classic view of economic decision theory [26] implies that decision-makers convert the value of different goods into a common scale of utility. Ecological [27], psychological [28] and neuroeconomic approaches [29] similarly suggest that the values of different types of reward are converted into a common currency. Rolls and Grabenhorst [1,3] have argued that different specific rewards must be represented on the same scale, but not converted into a common currency, as the specific goal selected must be the output of the decision process so that the appropriate action for that particular goal can then be chosen [1,3]. The key difference between the two concepts of common currency and common scaling lies in the specificity with which rewards are represented at the level of single neurons. Whereas a common currency view implies convergence of different types of reward onto the same neurons (a process in which information about reward identity is lost), a common scaling view implies that different rewards are represented by different neurons (thereby retaining reward identity in information processing), with the activity of the different neurons scaled to be in the same value range.

A recent functional magnetic resonance imaging (fMRI) study demonstrated the existence of a region in the human OFC where activations are scaled to the same range as a function of pleasantness for even fundamentally different

Box 2. Cost-benefit analysis for decision-making: extrinsic and intrinsic costs

If the OFC and ACC encode the value of sensory stimuli, does neural activity in these structures also reflect the cost of rewards? We propose that, when considering this, it is important to distinguish two types of cost. Extrinsic costs are properties of the actions required to obtain rewards or goals, for example physical effort and hard work, and are not properties of the rewards themselves (which are stimuli). By contrast, intrinsic costs are properties of stimuli. For example, many rewards encountered in the world are hedonically complex stimuli containing both pleasant and unpleasant components at the same time, for example: natural jasmine odor contains up to 6% of the unpleasant chemical indole; red wines and leaves contain bitter and astringent tannin components; and dessert wines and fruits can contain unpleasant sulfur components. Furthermore, cognitive factors can influence intrinsic costs, for example when knowledge of the energy content of foods modulates their reward value. Intrinsic costs can also arise because of the inherent delay or low probability/high uncertainty in obtaining them.

We suggest that intrinsic costs are represented in the reward-pleasure systems in the brain, including the OFC, where the values of stimuli are represented, and that extrinsic costs are represented in brain systems involved in linking actions to rewards, such as the cingulate cortex. Evaluation of stimulus-intrinsic benefits and costs appears to engage the OFC [55,95,96]. For example, in a recent fMRI study, it was found that the medial OFC, which represents the pleasantness of odors, was sensitive to the pleasant components in a naturally complex jasmine olfactory mixture, whereas the lateral OFC, which represents the unpleasantness of odors, was sensitive to the unpleasant component (indole) in the mixture [95]. A recent neurophysiological study found that reward risk and value are encoded by largely separate neuronal populations in the OFC [97]. The implication is that both reward value and intrinsic cost stimuli are represented separately in the OFC. This might provide a neural basis for processing related to cognitive reasoning about reward value and its intrinsic cost, and for differential sensitivity to rewards and aversion to losses. By contrast, a role for the cingulate cortex in evaluating the physical effort associated with actions has been demonstrated in studies in rats, monkeys [98] and humans [99]. Interestingly, single neurons in the lateral prefrontal cortex encode the temporally discounted values of choice options, suggesting that reward and delay costs are integrated in this region [100].

primary rewards: taste in the mouth and warmth on the hand [30] (Figure 2c). A different study found that the decision value for different categories of goods (food, non-food consumables and monetary gambles) during purchasing decisions correlated with activity in the adjacent ventromedial prefrontal cortex [VMPFC (the term 'VMPFC' is used to describe a large region of the medial prefrontal cortex that includes parts of the medial OFC, ACC and the medial prefrontal cortex area 10)] [31]. Importantly, because of the limited spatial resolution of fMRI, these studies are unable to determine whether it is the same or different neurons in these areas that encode the value of different rewards. However, as shown most clearly by single-neuron recording studies, the representations in the OFC provide evidence about the exact nature of each reward [1,3,22] (see the supplementary material online). Moreover, in economic decision-making, neurons in the macaque OFC encode the economic value of the specific choice options on offer, for example different juice rewards [2]. For many of these 'offer value' neurons, the relationship between neuronal impulse rate and value was invariant with respect to the different types of juice that were available [32], suggesting that different types of juice are evaluated on a common value scale.

With current computational understanding of how decisions are made in attractor neural networks [33–36] (see below), it is important that different rewards are expressed on a similar scale for decision-making networks to operate correctly but retain information about the identity of the specific reward. The computational reason is that one type of reward (e.g. food reward) should not dominate all other types of reward and always win in the competition, as this would be maladaptive. Making different rewards approximately equally rewarding makes it probable that a range of different rewards will be selected over time (and depending on factors such as motivational state), which is adaptive and essential for survival [3]. The exact scaling into a decision-making attractor network will be set by the number of inputs from each source, their firing rates and the strengths of the synapses that introduce the different inputs into the decision-making network [7,33,35,36]. Importantly, common scaling need not imply conversion into a new representation that is of a common currency of general reward [1]. In the decision process itself, it is important to know which reward has won, and the mechanism is likely to involve competition between different rewards represented close together in the cerebral cortex, with one of the types of reward winning the competition, rather than convergence of different rewards onto the same neuron [3,7,33,35,36].

The OFC and ACC represent value on a continuous scale, and not choice decisions between different value signals
To test whether the OFC and ACC represent the value of stimuli on a continuous scale and, thus, provide the evidence for decision-making, or instead are implicated themselves in making choices, Grabenhorst, Rolls *et al.* performed a series of investigations in which the valuation of thermal and olfactory stimuli in the absence of choice was compared with choice decision-making about the same stimuli. Whereas activation in parts of the OFC and ACC represented the value of the rewards on a continuous scale [10,37], the next connected area in the system, VMPFC area 10 (Figure 1), had greater activations when choices were made, and showed other neural signatures of decision-making indicative of an attractor-based decision process, as described below for Tier 3 processing [38,39] (Figure 3d).

Absolute value and relative value are both represented in the OFC

For economic decision-making, both absolute and relative valuation signals have to be neurally represented. A representation of the absolute value of rewards is important for stable long-term preferences and consistent economic choices [32,40]. Such a representation should not be influenced by the value of other available rewards. By contrast,

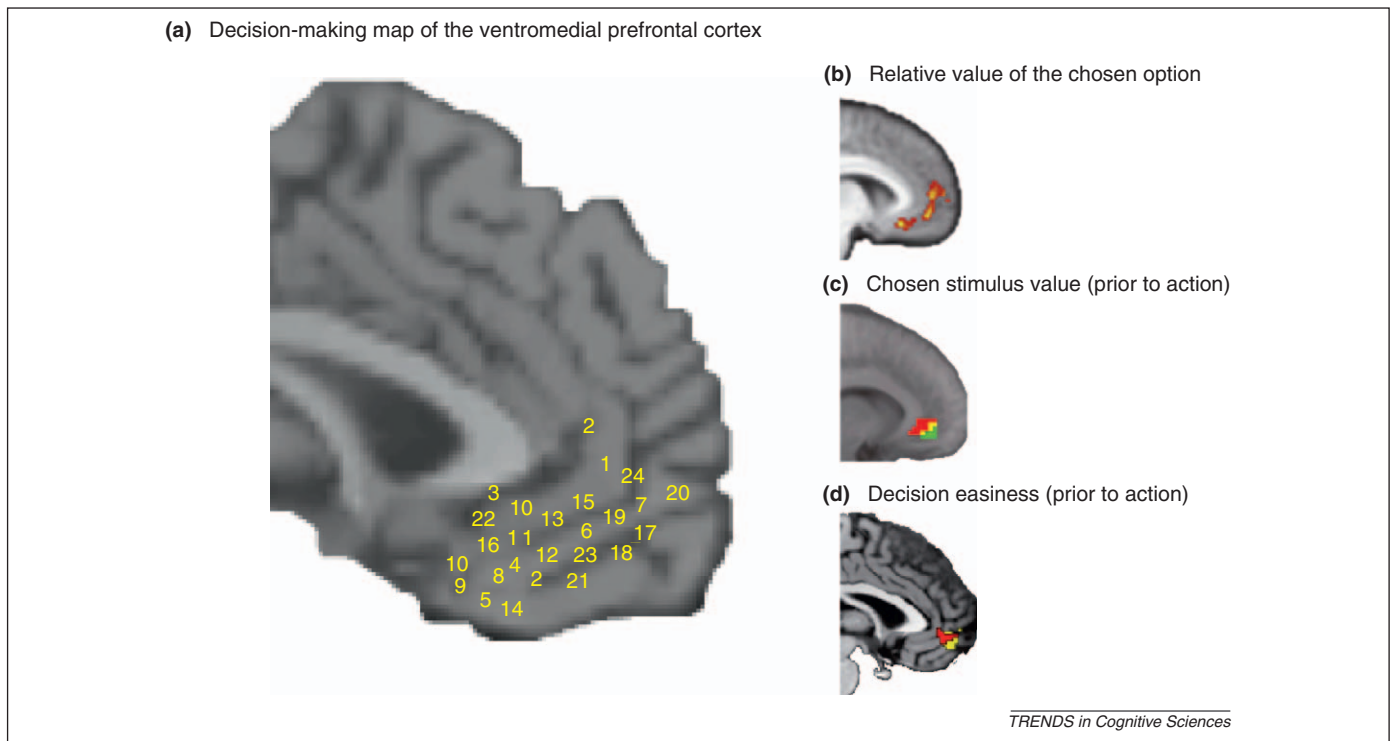


Figure 3. From value to choice in the VMPFC. (a) Activations associated with 1: (economic) subjective value during intertemporal choice; 2: immediate versus delayed choices; 3: immediate versus delayed primary rewards; 4: expected value during probabilistic decision-making; 5: expected value based on social and experience-based information; 6: expected value of the chosen option; 7: price differential during purchasing decisions; 8: willingness to pay; 9: goal value during decisions about food cues; 10: choice probability during exploitative choices; 11: conjunction of stimulus- and action-based value signals; 12: goal value during decisions about food stimuli; 13: willingness to pay for different goods; 14: willingness to pay for lottery tickets; 15: subjective value of charitable donations; 16: decision value for exchanging monetary against social rewards; 17: binary choice versus valuation of thermal stimuli; 18: binary choice versus valuation of olfactory stimuli; 19: easy versus difficult binary choices about thermal stimuli; 20: easy versus difficult binary choices about olfactory stimuli; 21: value of chosen action; 22: difference in value between choices; 23: prior correct signal during probabilistic reversal learning; and 24: free versus forced charitable donation choices. It is notable that some of the most anterior activations in VMPFC area 10 (activations 17–19) were associated with binary choice beyond valuation during decision-making. (See supplementary material online for references to the original studies.) (b) VMPFC correlates of the relative value of the chosen option during probabilistic decision-making. (c) VMPFC correlates of the chosen stimulus value are present even before action information is available [72]. (d) VMPFC correlates of value difference, and thus decision easiness and confidence, during olfactory and thermal value-based choices. Effects in this study were found in the far anterior VMPFC, medial area 10, but not in the OFC or ACC. Reproduced, with permission, from [70] (b), [72] (c), and [38] (d).

to select the option with the highest subjective value in a specific choice situation, the relative value of each option needs to be represented. A recent study provided evidence for absolute value coding in the OFC, in that neuronal responses that encoded the value of a specific stimulus did not depend on what other stimuli were available at the same time [32]. It was suggested that transitivity, a fundamental trait of economic choice, is reflected by the neuronal activity in the OFC [32]. This type of encoding contrasts with value-related signals found in the parietal cortex, where neurons encode the subjective value associated with specific eye movements in a way that is relative to the value of the other options that are available [41]. The apparent difference in value coding between the OFC and parietal cortex has led to the suggestion that absolute value signals encoded in the OFC are subsequently rescaled in the parietal cortex to encode relative value to maximize the difference between the choice options for action selection [41]. However, there is also evidence for the relative encoding of value in the OFC, in that neuronal responses to a food reward can depend on the value of the other reward that is available in a block of trials [42]. Two recent studies demonstrated that neurons in the OFC adapt the sensitivity with which reward value is encoded to the range of values that are available at a given time [43,44] (Figure 2c). This reflects an adaptive scaling of reward value, evident also in positive and negative contrast effects, that makes the system optimally sensitive to the local reward gradient, by dynamically altering the sensitivity of the reward system so that small changes can be detected [3]. The same underlying mechanism may contribute to the adjustment of different types of reward to the same scale described in the preceding section.

Given that representations of both absolute value and relative value are needed for economic decision-making, Grabenhorst and Rolls [45] tested explicitly whether both types of representation are present simultaneously in the human OFC. In a task in which two odors were successively delivered on each trial, they found that blood oxygenation level-dependent (BOLD) activations to the second odor in the antero-lateral OFC tracked the relative subjective pleasantness, whereas activations in the medial and mid-OFC tracked the absolute pleasantness of the second odor. Thus, both relative and absolute subjective value signals, both of which provide important inputs to decision-making processes, are separately and simultaneously represented in the human OFC [45].

Cognitive and attentional influences on value: a biased activation theory of top-down attention

How do cognition and attention affect valuation and neural representations of value? One possibility is that value representations ascend from the OFC and ACC to higher language-related cortical systems, and there become entwined with cognitive representations. In fact, there is a more direct mechanism. Cognitive descriptions at the highest, linguistic level of processing (e.g. 'rich delicious flavor') or attentional instructions at the same, linguistic level (e.g. 'pay attention to and rate pleasantness' vs 'pay attention to and rate intensity') have a top-down modulatory influence on value representations in the OFC and ACC of odor [46], taste and

flavor [6], and touch [47] stimuli by increasing or decreasing neural responses to these rewards. Thus, cognition and attention have top-down influences on the first part of the cortex in which value is represented (Tier 2), and modulate the effects of the bottom-up sensory inputs.

Recent studies have identified the lateral prefrontal cortex (LPFC, a region implicated in attentional control; Figure 1 [7,48]) as a site of origin for these top-down influences. In one study, activity in the LPFC correlated with value signals in the ventral ACC during self-controlled choices about food consumption [49]. Grabenhorst and Rolls have shown recently with fMRI connectivity analyses that activity in different parts of the LPFC differentially correlated with activations to a taste stimulus in the OFC or anterior insula, depending on whether attention was focused on the pleasantness or intensity of the taste, respectively [50]. Because activations of connected structures in whole cortical processing streams were modulated, in this case the affective stream (Tier 2 of Figure 1, including the OFC and ACC) versus the discriminative (object) stream (Tier 1 of Figure 1, including the insula), Grabenhorst and Rolls extended the concept of biased competition [51] and its underlying neuronal mechanisms [52] in which top-down signals operate to influence competition within an area implemented through a set of local inhibitory interneurons, to a biased activation theory of top-down attention [50], in which activations in whole processing streams can be modulated by top-down signals (Figure 4c).

These insights have implications for several areas related to neuroeconomics and decision-making, including the design of studies in which attentional instructions might influence which brain systems become engaged, as well as situations in which affective processing might be usefully modulated (e.g. in the control of the effects of the reward value of food and its role in obesity and addiction) [3,7,53].

From valuation to choice in the ventromedial prefrontal cortex

The operational principles described above enable the OFC and ACC (Tier 2 in Figure 1) to provide value representations that are appropriately scaled to act as inputs into neural systems for economic decision-making, and to promote a progression through the reward space in the environment to find the range of rewards necessary for survival and reproduction [3]. We next consider how neural value representations are transformed into choices in the VMPFC. We describe evidence that choices are made in attractor networks with nonlinear dynamics, in which one of the possible attractor states, each biased by a different value signal, wins the competition implemented through inhibitory interneurons [36].

Neural activity in the VMPFC in neuroeconomic tasks

Studies based on neuroeconomic and computational approaches have revealed that neural activity in the VMPFC correlates with the expected value of choice options during decision-making (Figure 3) [41,54]. For example, subject-specific measures of the expected 'goal value' of choice options can be derived from observed

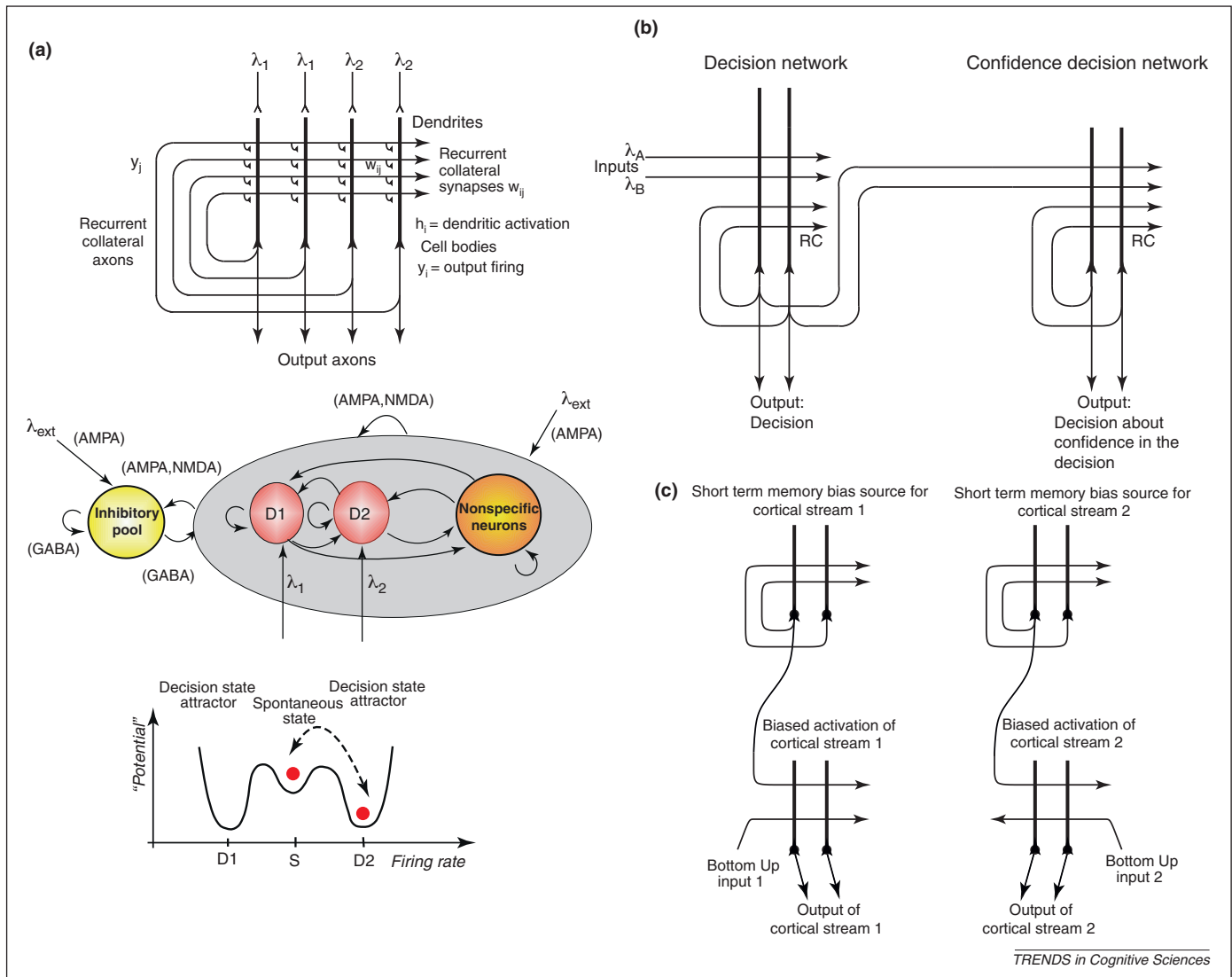


Figure 4. Decision-making and attentional mechanisms in the brain. **(a)** (top) Attractor or autoassociation single network architecture for decision-making. The evidence for decision 1 is applied via the λ_1 , and for decision 2 via the λ_2 inputs. The synaptic weights w_{ij} have been associatively modified during training in the presence of λ_1 and at a different time of λ_2 . When λ_1 and λ_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 times of the neurons (for a given mean rate) 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 (bottom), 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). (middle) The architecture of the integrate-and-fire network used to model decision-making. (bottom) 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 attractors that represents the decision. The noise in the network caused by the random spiking times of the neurons (for a given mean rate) 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 (bottom), 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)** A network for making confidence-based decisions. Given that decisions made in a first decision-making network have firing rates in the winning attractor that reflect the confidence in the first decision, a second 'monitoring' decision network can take confidence-related decisions based on the inputs received from the first decision-making network. The inputs to the decision-making network are λ_A and λ_B . A fixed reference firing rate input to the second, confidence decision, network is not shown. **(c)** A biased activation theory of attention. The short-term memory systems that provide the source of the top-down activations may be separate (as shown), or could be a single network with different attractor states for the different selective attention conditions. The top-down short-term memory systems hold what is being paid attention to active by continuing firing in an attractor state, and bias separately either cortical processing system 1, or cortical processing system 2. This weak top-down bias interacts with the bottom-up input to the cortical stream and produces an increase of activity that can be supralinear [52]. Thus, the selective activation of separate cortical processing streams can occur. In the example, stream 1 might process the affective value of a stimulus, and stream 2 might process the intensity and physical properties of the stimulus. The outputs of these separate processing streams must then enter a competition system, which could be, for example, a cortical attractor decision-making network that makes choices between the two streams, with the choice biased by the activations in the separate streams. (After Grabenhorst and Rolls 2010 [50].) Adapted, with permission, from [38] (aiii), [36] (b) and [50] (c).

choices between different rewards, such as when subjects bid money for goods they wish to acquire (i.e. willingness to pay), and these can be used as regressors for fMRI activity [31,49,55–57]. Using this approach, neural correlates of the goal value for different types of expected reward, including food items, non-food consumables, monetary gambles and lottery tickets, have been found in the VMPFC (Figure 3). Decision-related activity in the VMPFC is also found for choices about primary rewards, such as a pleasant warm or

unpleasant cold touch to the hand, and between olfactory stimuli [10].

As can be seen from Figure 3a, there is considerable variability in the exact anatomical location of decision-related effects in the VMPFC. Moreover, VMPFC activity has been linked to a wide range of valuation and choice signals that incorporates information about temporal delay [58–60], uncertainty [61], price or value differential [62,63], social advice [64], and monetary expected value

and reward outcome [24]. This heterogeneity of findings raises the question of whether a common denominator for the functional role of VMPFC in value-based decision-making can be identified or, alternatively, whether different VMPFC subregions make functionally distinct contributions to the decision-making process. A common theme that has emerged from the different strands of research is that the VMPFC provides a system for choices about different types of reward and for different types of decision, including in the social domain [64–67]. For example, Behrens and colleagues found that the VMPFC encoded the expected value of the chosen option based on the subjects' own experiences as well as on social advice [64].

On the basis of these findings, it has been suggested that the VMPFC represents a common valuation signal that underlies different types of decision as well as decisions about different types of goods [31,41,59,68]. A related account [69] suggests that, whereas the OFC is involved in encoding the value of specific rewards, the VMPFC plays a specific role in value-guided decision-making about which of several options to pursue by encoding the expected value of the chosen option [64,70,71]. Indeed, VMPFC activity measured with fMRI correlates with the value difference between chosen and unchosen options (i.e. relative chosen value), and this signal can be further dissected into separate value signals for chosen and unchosen options [70] (Figure 3b). However, with the temporal resolution of fMRI, it is difficult to distinguish input signals to a choice process (the expected or offer value, or value difference between options) from output signals of a choice process (the value of the chosen or unchosen option) and from those that represent the categorical choice outcome (the identity of the chosen option).

Value in the OFC and choice in VMPFC area 10

Rolls, Grabenhorst and colleagues have proposed an alternative account [1,10,36,38,39] that suggests that, whereas the OFC and ACC parts of the VMPFC are involved in representing reward value as inputs for a value-based choice process, the anterior VMPFC area 10 is involved in choice decision-making beyond valuation, as has been found in studies that have contrasted choice with valuation [10,37] (Figure 3d). Part of this proposal is that area 10 is involved in decision-making beyond valuation by implementing a competition between different rewards, with the computational mechanism described below. This choice process operates on the representation of rewarding stimuli (or goods, in economic terms) and, thus, occurs before the process of action selection. This is based, in part, on the evidence that neuronal activity in the OFC is related to the reward value of stimuli, and that actions such as whether any response should be made, or a lick response, or a touch response [3,7], or a right versus left response [2], are not represented in the OFC [3]. Indeed, using an experimental design that dissociated stimulus and action information in a value-based choice task, Wunderlich *et al.* demonstrated that correlates of the value of the chosen stimulus can be found in the VMPFC even before action information is available [72] (Figure 3c). Thus, we suggest that the role of the anterior VMPFC area 10 is to transform a continuously scaled representation of expected value (or offer

value) of the stimulus choice options into a categorical representation of reward stimulus choice. This process uses a mechanism in which the winner in the choice competition is the chosen stimulus, which can then be used as the goal for action to guide action selection.

This computational view on the role of the VMPFC in decision-making is fundamentally different from the proposal made by Damasio and colleagues, in which the VMPFC is involved in generating somatic markers (changes in the autonomic, endocrine and skeletomotor responses), which are then sensed in the insular and somatosensory cortices and thereby reflect the value of choice options and 'weigh in' on the decision process [73], as has been discussed in detail elsewhere [3].

Computational mechanisms for choice and their neural signatures

Phenomenological approaches

By examining computational models of decision-making, we now consider the processes by which the brain may make choices between rewards. One approach, which has been used mainly in the domain of sensory decision-making, can be described as phenomenological, in that a mathematical model is formulated without specifying the underlying neural mechanisms. The main such approach is the accumulator or race model, in which the noisy (variable) incoming evidence is accumulated or integrated until some decision threshold is reached [74]. This provides a good account of many behavioral aspects of decision-making, but does not specify how a mechanism for choice could be implemented in a biologically realistic way in the brain.

Choice implemented by competition between attractor states in cortical networks

A different approach is to formulate a theory at the mechanistic level of the operation of populations of neurons with biologically plausible dynamics of how choices are made in the brain (Figure 4) [33–36,75]. In this scenario, the parameters are given by the time constants and strengths of the synapses and the architecture of the networks; neuronal spiking occurring in the simulations provides a source of noise that contributes to the decision-making being probabilistic and can be directly compared with neuronal activity recorded in the brain; and predictions can be made about the neuronal and fMRI signals associated with decision-making, which can be used to test the theory. Interestingly, the theory implements a type of nonlinear diffusion process that can be related to the linear diffusion process implemented by accumulator or race models [76]. Furthermore, the degree of confidence in one's decisions and other important properties of a decision-making process, such as reaction times and Weber's Law, arise as emergent properties of the integrate-and-fire attractor model summarized in Figure 4 [33,36].

Predictions of the noisy attractor theory of decision-making

The attractor-based integrate-and-fire model of decision-making makes specific predictions about the neuronal signature of a choice system in the brain, including higher neuronal firing, and correspondingly larger fMRI BOLD

signals, on correct than error trials. The reason for this is that the winning attractor on a given trial (say attractor 1 selected as a consequence of a larger λ_1 than λ_2 and the noise in the system caused by the randomness in the neuronal spiking times for a given mean rate) receives additional support from the external evidence that is received via λ_1 on correct trials [36,39,75]. For the same reason, on correct trials, as the difference $\Delta\lambda$ between λ_1 and λ_2 increases, so the firing rates and the predicted fMRI BOLD signal increase. Rolls *et al.* have recently confirmed this prediction for VMPFC area 10 when choices were being made between the pleasantness of successive odors [39]. Conversely, but for the same reason, on error trials, as $\Delta\lambda$ increases, so the firing rates and the predicted fMRI BOLD signal decrease [39]. This prediction has also been confirmed for area 10 [39]. If all trials, both correct and error, are considered together, then the model predicts an increase in the BOLD signal in choice decision-making areas, and this prediction has been confirmed for area 10 [38,39]. (Indeed, this particular signature has been used to identify decision-making areas of the brain, even though there was no account of why this was an appropriate signature [77].) The confirmation of these predictions for area 10, but not for the OFC where the evidence described above indicates that value is represented, provides strong support for this neuronal mechanism of decision-making in the brain [38,39].

The same neuronal cortical architecture for decision-making (Figure 4) is, Rolls and Deco propose [36], involved in many different decision-making systems in the brain, including vibrotactile flutter frequency discrimination in the ventral premotor cortex [35], optic flow in the parietal cortex and the confidence associated with these decisions [78], olfactory confidence-related decisions in the rat prefrontal cortex [79,80] and perceptual detection [36]. A useful property of this model of decision-making is that it maintains as active the representation of the goal or state that has been selected in the short-term memory implemented by the recurrent collateral connections, providing a representation for guiding action and other behavior that occurs subsequent to the decision [36]. In a unifying computational approach, Rolls and Deco [36] argue that the same noise-influenced categorization process also accounts for memory recall, for the maintenance of short-term memory and therefore attention, and for the way in which noise affects signal detection. Furthermore, disorders in the stability of these stochastic dynamical cortical systems implemented by the recurrent collateral excitatory connections between nearby cortical pyramidal cells, contribute to a new approach to understanding schizophrenia (in which there is too little stability) [81,82] and obsessive-compulsive disorder (in which it is hypothesized that there is too much stability) [83].

Confidence in decisions

As the evidence for a decision becomes stronger, confidence in the decision being correct increases. More formally, before the outcome of the decision is known, confidence in a correct decision increases with $\Delta\lambda$ on correct trials, and decreases on trials when an error has in fact been made [84]. The model just described accounts for confidence in decisions as an emergent property of the attractor network

processes just described, with the firing rates and predicted BOLD signals reflecting confidence, just as they do $\Delta\lambda$ on correct than error trials.

If one does not have confidence in an earlier decision then, even before the outcome is known, one might abort the strategy and try the decision-making again [79]. The second decision can be modeled by a second decision-making network that receives the outputs from the first decision-making network [36,80] (see Figure 4b). If the first network in its winning attractor has relatively high firing rates reflecting high confidence in a correct decision, then the second network can use these high firing rates to send it into a decision state reflecting 'confidence in the first decision'. If the first network in its winning attractor has relatively lower firing rates reflecting low confidence in a correct decision, then the second network can use these lower firing rates to send it into a decision state reflecting 'lack of confidence in the first decision' [80].

This two-decision network system (Figure 4b) provides a simple model of monitoring processes in the brain, and makes clear predictions of the neuronal activity that reflects this monitoring process [36,80]. Part of the interest is that 'self-monitoring' is an important aspect of some approaches to consciousness [85,86]. However, we think that it is unlikely that the two attractor network architecture would be conscious [36].

Concluding remarks and future priorities

We have linked neurophysiological and neuroimaging to computational approaches to decision-making and have shown that representations of specific rewards on a continuous and similar scale of value in the OFC and ACC (Tier 2) are followed by a noisy attractor-based system for making choices between rewards in VMPFC area 10 (Tier 3). Subjective pleasure is the state associated with the activation of representations in Tier 2, and confidence is an emergent property of the decision-making process in Tier 3. Similar neuronal choice mechanisms in other brain areas are suggested to underlie different types of decision, memory recall, short-term memory and attention, and signal detection processes, and for some disorders in these processes.

In future research, it will be important to examine how well this stochastic dynamical approach to decision-making, memory recall, and so on, can account for findings in many brain systems at the neuronal level; how subjective reports of confidence before the outcome is known are related to neural processing in these different brain systems; how this stochastic dynamic approach to decision-making may be relevant to economic decision-making [87,88]; and whether this approach helps to understand and treat patients, for example those with damage to the brain that affects decision-making, and those with schizophrenia and obsessive-compulsive disorder.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.tics.2010.12.004](https://doi.org/10.1016/j.tics.2010.12.004).

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