



Review

Neural representations of subjective reward value

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ABSTRACT

Decision neuroscience suggests that there exists a core network for the subjective valuation of rewards from a range of different domains, encompassing the ventral striatum and regions of the orbitofrontal cortex (OFC), in particular the ventromedial aspect of the OFC. Here we first review ways to measure subjective value experimentally in a cognitive neuroscience context, and provide a brief overview over different types of value (outcome, goal and decision value). We then compare results of functional neuroimaging studies of subjective value representations across these different types of value. Our analysis suggests that the same region of the mOFC represents the outcome values of primary reinforcers, but also more complex decision values in which multiple dimensions of the reward need to be integrated. The subjective (hedonic) experience of processing highly valued decision options (regardless of whether they refer to actually experienced rewards or merely potential future rewards) appears to be what is reflected in value-related mOFC activity.

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Contents

1. Introduction.....	135
2. Brief taxonomy of value types.....	136
2.1. Outcome value.....	136
2.2. Goal value.....	136
2.3. Decision value.....	136
2.4. Action value.....	137
3. Neural representations of subjective value.....	137
3.1. Anatomy of the reward system.....	137
3.1.1. The ventral striatum.....	137
3.1.2. The orbitofrontal cortex.....	137
3.2. Neural value representations.....	138
3.2.1. Differential roles for the VS and OFC.....	139
3.2.2. Differential roles for the medial and lateral OFC.....	139
3.2.3. Decision costs and subjective hedonic experience.....	140
4. Conclusions.....	140
References.....	140

1. Introduction

The idea that the brain represents the value of environmental stimuli in an abstract code is central to the fields of decision neuroscience and neuroeconomics [42]. The rationale behind this assumption is straightforward—an abstract representation of the value of a given stimulus allows an agent to readily compare stimuli from different domains in order to initiate approach or avoidance

behaviour. When choosing between a small and a large amount of food, it may be sufficient to rely on within-domain value representations (for example within a certain sensory system). However, this situation changes when the agent is faced with, e.g. the choice between a primary and a secondary reinforcer such as between money and food. In this situation, it is generally assumed that both rewards are mapped onto comparable neural representations of value, thus enabling the agent to choose whichever reinforcer best serves the current goals of the agent. However, this situation becomes even more complex when rewards are associated with different types of costs (such as uncertainties, delays or effort requirements), as such costs lead to a reduction in the value that

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agents place on rewards (referred to as reward discounting), which depends greatly on subjective preferences. Most of our choices are of the latter type—in real life, rewards are almost always uncertain or delayed and are rarely obtained without effort. This high ecological relevance of value-based decision making has recently led to increased research into underlying neural mechanisms.

The present review has two main aims. Firstly, we will briefly introduce different subtypes of value and give some examples of how they can be measured experimentally. Then, we will review the evidence in favour of the view that a single mesocorticolimbic system, including the ventral striatum and parts of the orbitofrontal cortex, represents both different subtypes of value and the values of different classes of reinforcers. In this section, we will also speculate on which anatomical connections may underlie the value sensitivity of these regions.

2. Brief taxonomy of value types

Many earlier neuroimaging studies of reward processing have focussed on objective properties of rewards, such as magnitude or probability [46,47,79,80]. However, how objective reward properties such as probabilities are incorporated into the choice process varies considerably between individuals. Therefore, the search for neural representations of subjective value requires that accurate estimates of subjective value can be inferred experimentally. Only then can these value estimates be correlated with electrophysiological responses or blood-oxygenation-dependent (BOLD) signals that are measured using functional magnetic resonance imaging (fMRI).

Different types of values have been proposed in decision neuroscience, including goal value, decision value, outcome value and action value [11,37,67,78]. The following summary does not claim to be exhaustive. Rather, we aim to provide a brief overview of these different types of value, and briefly outline ways to measure them experimentally.

2.1. Outcome value

The outcome value of a stimulus (OV) is perhaps the most basic type of value, as it refers to the value of a reinforcer upon consumption. For primary reinforcers such as food, this is illustrated by the idea that, all else being equal, the OV of consuming a glass of Chardonnay is, for most people, likely to be greater than that of a glass of water. Importantly, OVs are unrelated to costs or efforts associated with obtaining rewards. They merely reflect the strength of a reinforcer as it is consumed.

Subjective outcome value of primary reinforcers is often measured using simple ratings. For example, Krangelbach et al. [50] scanned subjects in an fMRI block-design while they consumed different liquid food stimuli (tomato juice, chocolate milk or a tasteless control solution). At different times during the experiment, participants were asked to rate the pleasantness of the different liquids. Because the pleasantness of consuming the different liquids changed over the course of the experiment, due to feeding of the subjects to satiety, the authors were able to correlate subjective pleasantness ratings to BOLD activity measured using fMRI. Similar approaches have been adopted in the study of olfaction [2], gustation [15,26,66] and attractiveness/likeability of visual stimuli [19,52,57]. While it is essential to rely on such ratings to obtain subjective measures of outcome value, there is a difficulty associated with this approach. Because subjective ratings do not entail behavioural consequences, participants have no intrinsic motivation to respond accurately other than to comply with the instructions of the experimenter. An alternative approach is to measure value based on the actual choice behaviour of the agent.

2.2. Goal value

The GV of a stimulus is similar to the OV in that it does not include costs. However, the GV is not as directly related to the consumption of a reward, but somewhat more abstract in nature—it refers to the value of a stimulus in units of a more abstract currency. In a seminal study [61] monkeys were trained to choose between different quantities of two different juices (A and B), e.g. 3 units of A vs. 6 units of B, or 2 units of A vs. 3 units of B. Behaviourally, the monkeys did not simply opt for the larger quantity of juice, but rather showed a subject-specific trade-off between juice type and juice quantity. By fitting sigmoid functions to the choice data of each individual, the authors were able to determine the quantity difference between A and B at which monkeys were indifferent between the two available options (the so-called indifference point), effectively putting juices A and B on the same scale. The GV of the different options was thus quantified solely based on the actual choice behaviour of the monkeys, and the authors then used this abstract measure of GV to model electrophysiological data recorded in the orbitofrontal cortex (OFC).

In humans, GV is often quantified by asking participants how much money they would be willing to pay for certain items [37,65,76] or by measuring how much effort they are willing to invest to obtain a specific reinforcer [62,74]. In the former type of studies, participants are given an initial monetary endowment, and then bid amounts b on a range of different goods while brain activity is measured using fMRI [11,36,37,65]. At the end of the experiment, one trial is randomly selected and played out according to a Becker–DeGroot–Marschak (BDM) auction [4], with the following rules. For a given selected auction, a number n is randomly selected from a known distribution (e.g. if subjects were initially allowed to bid 0, 1, 2 or 3 dollars, one of these numbers would be randomly drawn). If $b \geq n$, the participant receives the item for a price of n dollars. On the other hand, if $n > b$, the participant does not receive the object but also does not pay anything. The best strategy is to bid exactly the amount that one is willing to pay for each item, the so-called willingness-to-pay [WTP] [65,76]. The actual price is determined by the random number n , so there is no reason to bid less than the actual WTP. Therefore, the bids in these types of auctions directly reflect the (subjective) GV of the items and can, similar to the subjective ratings described above, be used for fMRI analyses of neural value signals. Furthermore, the bids are behaviourally relevant, because typically, at the end of the scanning session, one trial is randomly selected, and the corresponding auction actually takes place. Motivation can be additionally increased by asking subjects not to eat for a couple of hours and then have them bid on food snacks [36,65]. Reinforcers for which subjects are willing to give more money (or invest more effort) have by definition a greater GV. Furthermore, through their respective GVs, an agent can compare reinforcers from different domains. It should also be noted that GV and OV are highly correlated, the main difference being that the former are expressed in terms of abstract units, whereas the latter are not.

2.3. Decision value

DV refers to the net value of a specific decision option that is under consideration by the agent. In contrast to GV and OV, the DV includes costs. Thus, the DV of a delayed reward is lower than the DV of an immediate reward of the same magnitude, and the DV of a probabilistic reward is lower than that of a certain reward of the same magnitude, and so forth. All costs lead to a reduction (discounting) of value. The DV of a glass of Chardonnay priced at 4€ is lower than that of the same wine available for just 3€—the DV is the GV minus the sum of the costs. Importantly, however, not all individuals incorporate costs into the DV in the same way—risk-averse

agents may discount risky rewards more, whereas other agents may discount delayed rewards less. Therefore, the decision value of an option depends on the costs and the associated reward, which are integrated by means of a subject-specific value function. For a range of decision costs, there are good behavioural models of how humans and animals incorporate these costs into their value function, in particular with respect to delays and uncertainties. Value is discounted over time [32], and a single parameter hyperbolic function can accurately account for choice between immediate and delayed rewards. Differences in the rate of discounting reflect differences in subjective preferences, i.e. differences in the DV that different individuals assign to delayed rewards. While agents with a low temporal discount rate are willing to wait for a long time to obtain small additional payoffs, impatient agents with a high discount rate are unwilling to even wait for short periods of time to obtain large additional rewards. Thus, the same decision option may have a large DV for a patient agent but an extremely low DV for an impatient agent. The same type of hyperbola also accounts for risky decision making (also referred to as probability discounting) [32]. A range of different, though only slightly modified models of delay and probability are discussed. For example, the variance accounted for in choice behaviour can be further increased by including an additional non-linear scaling parameter in the model [55,56]. Along similar lines, models can be constructed for other decision-making scenarios such as choice under ambiguity [24,39,53], where the probabilities of the different outcomes are not known.

Typically, such paradigms involve a large number of choices between a fixed reference reward and a range of probabilistic, ambiguous or delayed rewards [41,43,53,63]. Based on the actual choice data of subjects on these tasks, the best-fitting model parameters can be estimated, and the DV of each decision option that is being processed can be calculated. In such cases, the motivation (and ecological validity) of the task is typically increased by randomly selecting and paying out one (or a small number) of choices following the experiment. Such formal models of preferences are invaluable for the study of neural representations of value, because they provide accurate numerical estimates which can be used for data analysis. The subjective (discounted) values can be used to model fMRI data [41,63,64] or electrophysiological data [44,45].

2.4. Action value

Choice cannot be measured without action. Pre-choice, agents assign values to the different available actions [67,78] [action value AV] and then execute the action with the highest associated value. Depending on the complexity of the decision context, these values can be based on OV, GV or DV. AVs are therefore strictly speaking not a special type or class of values, but rather reflect the pairing of a particular action with a particular value, which can be OV, GV or DV. Of course, whenever different actions are associated with different effort requirements, the associated action values are by definition DVs rather than GVs or OVs, because effort requirements are incorporated into the value function.

3. Neural representations of subjective value

There is considerable evidence for the existence of a final common representation of value in the ventral striatum (VS) and the orbitofrontal cortex (OFC) [42], in particular its ventromedial portion. In the following section, we will focus on functional neuroimaging findings in humans regarding neural representations of value. Findings of reward-related processing in neuroimaging are increasingly related to primate neuroanatomy [33], and neuroimaging studies have investigated neural representations of all types of value discussed above (outcome, goal and decision value).

We will firstly review the available anatomical data regarding the connections of VS and OFC and then speculate how the information relayed to these regions may contribute to their role of value representations. We will also explore whether there is evidence for dissociable value representations in VS and sub-networks of the OFC for different types of value or different classes of reinforcers.

3.1. Anatomy of the reward system

3.1.1. The ventral striatum

The ventral striatum (VS) is part of the basal ganglia, encompassing ventral parts of the caudate and the nucleus accumbens (Nacc). In a seminal study, it was shown that rats will work for electrical stimulation of the Nacc [59], providing strong evidence for a role of the Nacc in positive reinforcement.

The basal ganglia are generally organized into a more anterior limbic section, an associative loop, and a more posterior motor loop, with distinct topographical connectivity patterns with the neocortex [1]. The dorsal striatum receives sensory-motor input whereas the limbic striatum forms a central component of the brain's reward network. Midbrain regions such as the substantia nigra and the ventral tegmental area (VTA) give rise to a strong dopaminergic projection to the VS, which also sends projections back to these regions [18,38]. The amygdala also gives rise to projections to the VS, predominantly to the Nacc [23,73]. Hippocampal input to the VS also targets the Nacc and originates mainly in the rostral part of the hippocampal formation [22]. Finally, the VS receives strong thalamic input. Importantly, the limbic network of the ventromedial OFC also sends strong projections to the Nacc (see below).

The most pronounced output projections of the VS target more posterior regions of the basal ganglia such as the pallidum, from which, via the thalamus, information is relayed back to the neocortex [68]. The VS also sends projections directly to the dopaminergic midbrain (see above). Importantly, the VS may also exert a direct, non-thalamic influence on information processing in limbic regions such as the amygdala through its output projections to the bed nucleus of the stria terminalis and the nucleus basalis [34].

3.1.2. The orbitofrontal cortex

The OFC is located in the ventral part of the frontal lobes, and can be divided into a sensory network (also referred to as the lateral or orbital network of the OFC) and a limbic network (also referred to as the medial network), based on anatomical connectivity data [60]. The medial OFC is densely connected with limbic regions such as the hippocampus, perirhinal/parahippocampal cortices and amygdala [8] and to posterior midline structures such as the posterior cingulate and retrosplenial cortices [10]. Limbic projections to lateral OFC, on the other hand, are largely confined to the amygdala [8]. The lateral, but not the medial OFC, receives predominantly sensory information [9]. Inputs from a given sensory modality converge on distinct subregions of the lateral OFC, with more diffuse sensory inputs being considerably lighter. Distinct subregions of the lateral OFC thus receive visual, auditory, olfactory, gustatory, somatosensory and visceral input [51]. Regarding cortico-cortical connections of the PFC, dorsolateral and ventrolateral PFC regions may influence information processing in the OFC through top-down projections [3].

The medial and lateral networks also differ with respect to their connections to the VS. While the medial OFC predominantly projects to the VS (i.e. the caudate nucleus and the Nacc), the lateral network projects to more posterior regions of the striatum [20]. Finally, the major cortical projection to visceral brainstem regions originates from the medial OFC.

Table 1
Studies investigating subjective value representations using functional neuroimaging included in the present review. Activations with an x-coordinate between –10 and +10 were classified as mOFC. More lateral peaks were classified as lateral/central OFC.

Study	Value measure	Value type	Reward type	mOFC/vmPFC	l/cOFC	VS
Outcome value						
Anderson et al. (2003) [2]	Rating	OV	Olfactory	–	X	–
Blood et al. (1999) [6]	Rating	OV	Music	–	X	–
Blood and Zatorre (2001) [5]	Rating	OV	Music	–	X	X
Cloutier et al. (2008) [12]	Rating	OV	Visual	X	–	X
de Araujo et al. (2003a) [15]	Rating	OV	Olfactory/gustatory	X	–	–
de Araujo et al. (2003b) [14]	Rating	OV	Gustatory	X	X	–
de Araujo et al. (2005) [16]	Rating	OV	Olfactory	X	X	–
Grabenhorst et al. (2007) [29]	Rating	OV	Gustatory	X	X	–
Grabenhorst and Rolls (2008) [27]	Rating	OV	Gustatory	X	–	–
Grabenhorst et al. (2008) [30]	Rating	OV	Somatosensory	X	–	–
Grabenhorst and Rolls (2009) [28]	Rating	OV	Olfactory	X	X	–
Grabenhorst et al. (2009) [31]	Rating	OV	Gustatory	–	X	–
Kringelbach et al. (2003) [50]	Rating	OV	Gustatory	–	X	–
Lebreton et al. (2009) [52]	Rating	OV	Visual	X	–	X
McClure et al. (2004), Exp. 1 [54]	Choice	OV	Gustatory	X	–	–
McClure et al. (2004), Exp. 2 [54]	Choice	OV	Gustatory	X	–	–
O'Doherty et al. (2003) [57]	Rating	OV	Visual	X	–	–
O'Doherty et al. (2006) [58]	Rating	OV	Gustatory	X	–	–
Plassmann et al. (2008) [66]	Rating	OV	Gustatory	X	–	–
Rolls et al. (2003) [71]	Rating	OV	Olfactory	X	–	–
Rolls and McCabe (2007), Group 1 [72]	Rating	OV	Gustatory	X	–	–
Rolls and McCabe (2007), Group 2 [72]	Rating	OV	Gustatory	X	–	–
Rolls et al. (2008) [70]	Rating	OV	Somatosensory	X	X	X
Small et al. (2001) [75]	Rating	OV	Gustatory	–	X	X
Winston et al. (2007) [77]	Rating	OV	Visual	X	–	–
			Total OV	72%	48%	16%
Goal value						
Chib et al. (2009) [11]	BDM	GV	Money	X	–	–
			Food snacks	X	–	–
			Trinket	X	–	–
Daw et al. (2006) [13]	Choice	GV	Points	X	X	–
DeMartino et al. (2009) [17]	BDM	GV	Lottery	X	–	–
Gläscher et al. (2009) [25]	Choice	GV	Money	X	–	–
Hare et al. (2008) [37]	BDM	GV	Food snacks	X	X	–
Hare et al. (2009) [36]	Rating	GV	Food snacks	X	–	–
Koeneke et al. (2008) [48]	Rating	GV	Food snacks	–	X	–
Plassmann et al. (2007) [65]	BDM	GV	Food snacks	X	–	–
			Total GV	90%	30%	0%
Decision value						
Fitzgerald et al. (2009) [21]	Choice	DV	Money/items	–	X	–
Hare et al. (2008) [37]	BDM	DV	Food snacks	–	X	–
Hare et al. (2010) [35]	BDM	DV	Donation	X	–	–
Kable and Glimcher (2007) [41]	DD	DV	Money	X	–	X
Kable and Glimcher (2010) [43]	DD	DV	Money	X	–	X
Levy et al. (2010) [53]	Risky	DV	Money	X	–	X
	Ambiguous	DV	Money	X	–	X
Peters and Büchel (2009) [63]	DD	DV	Money	X	X	X
	Risky	DV	Money	X	X	X
Peters and Büchel (2010) [64]	DD	DV	Money	–	X	X
			Money	–	X	X
			Total DV	63.6%	54.5%	72.7%
			Overall	76%	43.5%	28.3%

OV, outcome value; GV, goal value; DV, decision value; BDM, Becker–DeGroot–Marschak Auction; DD, delay discounting.

3.2. Neural value representations

Here we focussed on neuroimaging studies in which neuronal representations of subjective stimulus value were investigated. To this end, we only included studies in which subjective ratings, model-based value estimates or other subjective measures of value were correlated with neuroimaging data. Studies in which no continuous measure of value was obtained were not included in the analysis, such as cases in which only single binary preference judgements were made. In total, we examined activation peaks in the OFC and VS from 46 contrasts. Table 1 shows the percentages of contrasts yielding a particular activation peak separately for OV, GV and DV. A peak was classified as mOFC if the x-coordinate fell in the range [–10 to +10]. All more lateral OFC activations were classified

as lateral/central OFC, since a further distinction between lateral and central OFC did not seem feasible in the light of the relatively few studies investigated.

Across all 46 contrasts, mOFC activity was observed most frequently (76% of all contrasts), followed by lOFC (43.5%) and VS activation (28.3%). Relatively large proportions of contrasts for each type of value showed mOFC activation (OV: 72%, GV: 90%, DV: 63.6%). lOFC activation was observed less frequently, but also with similar frequency across value types (OV: 48%, GV: 30%, DV: 54.5%). VS activity, in contrast, was most frequently observed in DV contrasts, and much less in OV or GV contrasts (OV: 16%, GV: 0%, DV: 72.7%).

In light of previous findings suggesting anterior–posterior (abstract–concrete rewards) and medial–lateral (positive–negative

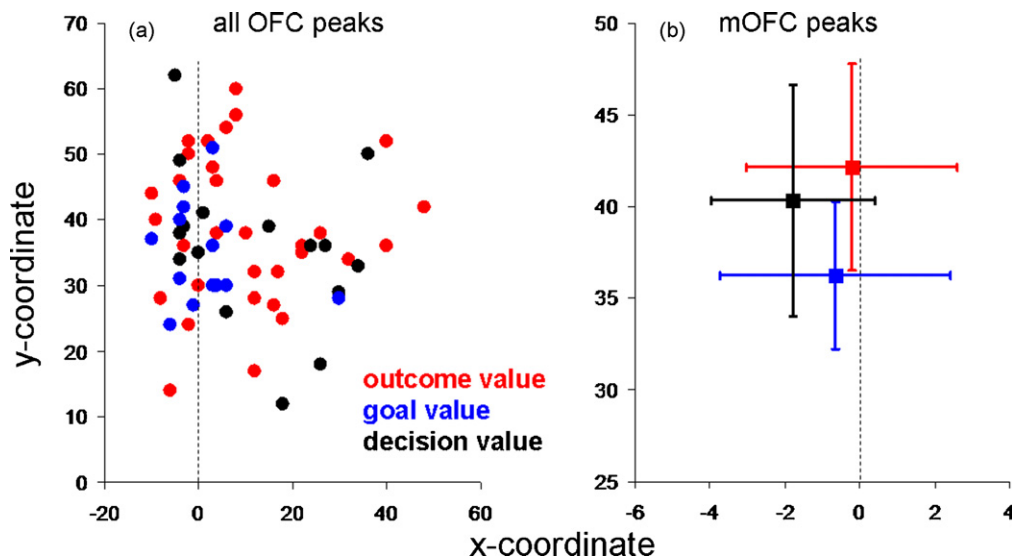


Fig. 1. (a) Peak coordinates (x–y dimension) for all activation peaks located in the OFC from contrasts listed in Table 1. A similar distribution of peaks was observed regardless of whether value representations reflected outcome, goal or decision values. Note that more peaks are plotted than contrasts listed in Table 1, because a number of contrasts included multiple peaks. (b) Very similar regions in the mOFC represent the subjective values of primary and secondary reinforcers, as well as goal or decision values (mean x- and y-coordinates and 95% confidence intervals are plotted in MNI space).

reinforcers) functional dissociations in the OFC [51], we next analyzed the OFC activation peaks as a function of location in the x–y dimension. Fig. 1a depicts the peak coordinates of all OFC peaks reported. For ease of comparison, the sign of the x-coordinate of all left lateralized lateral OFC clusters was flipped. As can be seen from Fig. 1a, no clear spatial dissociation as a function of value type emerged. For example, both more sensory OVs and more abstract DVs activated similar regions in the lateral OFC, even though this structure is has very pronounced connections with sensory cortices (see above).

We next focussed on activations in mOFC (Fig. 1b) and plotted the mean x–y-coordinates of all mOFC peaks, separately for each type of value (mean MNI x–y-coordinates OV: 0.42; GV: 0.37; DV: –1.38). It can be clearly seen from Fig. 1b that OVs, GVs and DVs were represented in a very similar region of the mOFC, suggesting that the degree to which values reflect sensory characteristics or more complex measures that include different types of decision costs appear not to influence/determine their neural representation in the mOFC. Furthermore, there was no evidence for an anterior–posterior dissociation, with more abstract reinforcers being represented in more anterior, and more sensory reinforcers being represented in more posterior regions of the mOFC, although this may be due to the fact that, in all investigated studies, subjects were required to make more or less explicit subjective evaluations [51,69].

3.2.1. Differential roles for the VS and OFC

While IOFC and mOFC showed somewhat similar patterns, VS activation was more pronounced for DV than OV or GV. It has recently been proposed that reward-related responses in the VS may reflect a prediction error rather than a value signal [37]. The present overview lends some support to this notion, as value signals in mOFC and IOFC were observed more frequently than value signals in the VS (see above). Nonetheless, although most studies listed in Table 1 included complete lists of activations, not all did. It is thus possible that some activations in VS may have not been reported because the authors focussed on responses in the OFC. Furthermore, effects of thresholding strongly influence a categorical overview such as the one in Table 1.

Nonetheless, it is of some interest that a considerable number of DV studies observed VS value signals, whereas few studies target-

ing OV and no study targeting GV did. At least three of the studies reporting DV signals in the VS report numerically higher correlations of VS activity with subjective value as compared to objective reward properties, such as amount, probability or expected value [41,53,63]. In conjunction with the finding that VS activity tracks individual, subject-specific distortions in the probability weighting function [40], these findings suggest that VS activation indeed reflect subjective aspects of rewards. One possibility would be that paradigms involving large numbers of trials, such as delay discounting tasks, may lead to a greater build-up of reward expectancies in participants, which may enhance prediction error related VS responses, which are difficult to dissociate from value-related responses.

3.2.2. Differential roles for the medial and lateral OFC

At first sight, the present overview appears to be somewhat at odds with the view that lateral OFC is more involved in coding for negative reinforcers, whereas medial OFC codes for positive reinforcers [51]. Although a greater percentage of studies observed mOFC value signals, IOFC activation was observed in slightly less than 50% of all contrasts. This observation does, however, not rule out an important role for the IOFC in representing negative reinforcers, but merely argues against the possibility that IOFC is not at all involved in the representation of positive reinforcers.

Despite the fact that the lateral OFC network (and not the medial network) has pronounced anatomical connections with sensory cortices, the value of primary reinforcers, which are by definition more grounded in the sensory domain, and secondary reinforcers such as money, appear to be represented in overlapping regions of the mOFC. The mOFC may thus play an important role in the subjective hedonic experience associated with processing highly valued stimuli [49]. This would also be in line with the findings that when attention is focussed on intensity rather than pleasantness of stimuli, mOFC value signals are reduced [27].

Whether value signals in the IOFC show a modality-dependent topographical distribution is of considerable interest in light of the modality-specific sensory inputs to the IOFC that terminate in distinct OFC subregions (see above). However, the relatively small number of studies investigating OV for modalities other than the olfactory/gustatory modality makes such an analysis currently unfeasible. Similarly, the view that more abstract reinforcers

are represented in more anterior parts of the mOFC, and more basal reinforcers in more posterior regions is not supported by this review, at least with respect to studies investigating subjective reward representations. Rather, the same mOFC region was observed to code for value of both primary and secondary reinforcers. In addition, our analyses suggest that this region does not distinguish the degree to which the represented value signal reflects the incorporation of different decision costs such as delays or probabilities.

3.2.3. Decision costs and subjective hedonic experience

If the mOFC signal represents subjective hedonic experience for a range of reinforcers, as the above analyses seem to suggest, the question arises where in the brain different decision costs are integrated into the value function. On the one hand, costs could be integrated into a value signal directly at the level of the mOFC. Thus, the mOFC may support the subjective hedonic experience of processing highly valued stimuli, but also, in the case of DVs, at the same time support the integration of decision costs into the value function. However, given that depending on the type of decision cost, very different mechanisms may be required for cost integration (such as mental simulation of future scenarios for delays, and processing of numerosities for probabilities [63]), it seems more likely (and efficient) that cost integration occurs in domain-specific, cortical networks that are specialized for processing particular types of cost information. Depending on subjective preferences, specialized cortical networks may therefore integrate reward costs into domain-specific subjective value signals [63].

While the previous considerations suggest a role of the mOFC in coding for subjective hedonic experience, the theoretical motivation for the assumption of a common neural value signal is based on the idea that such a signal may allow an organism to compare stimuli from different domains during choice [42]. To this end, the organism must in most cases rely on past experience and mental simulation. Therefore, this apparent discrepancy is easily resolved when one considers the fact that, in decision-making tasks usually adopted to measure DV or GV (see above), the hedonic experience is mostly hypothetical, such that the mere possibility of receiving a particular highly valued reward yields activation in the OFC. This is supported by recent data showing that the same mOFC region responds to real monetary rewards and imagery of reward episodes [7]. Thus, these considerations suggest a role of the mOFC in both actually experienced (as in the processing of OV) and merely mentally simulated (as in the processing of DV and GV) hedonic experiences. mOFC recruitments of the latter type may thus enable cross-domain value comparisons.

4. Conclusions

Taken together, we confirm that there is considerable evidence for a common coding of subjective value in the mOFC, and to a lesser extent in the IOFC and VS. Our survey of neuroimaging studies of subjective value representations shows that an overlapping region of the mOFC represents subjective value regardless of whether this value is derived via complex computations in which different properties of the reward (such as delays, probabilities or ambiguities) are integrated, or whether the pleasantness of a primary reinforcer is simply evaluated by a subject. Overall, the current literature is compatible with the idea that the mOFC supports the subjective hedonic experience during processing of highly rewarding stimuli from a range of different domains. The fact that the OFC represents both OVs and DVs/GVs furthermore suggests a role of this structure in mental simulation of reward outcomes, because the decision options in DV and GV paradigms (see Section 2) usually refer to possible or potential reward outcomes, and not to actually experienced outcomes. The fact that the OFC may jointly represent

such potential reward outcomes and actually experienced reward episodes (such as the perception of a pleasant taste, smell, touch or image) reconciles the subjective hedonic experience view of mOFC function [49] with the theoretical idea that a common neural value signal may enable choices between stimuli from different domains [42].

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