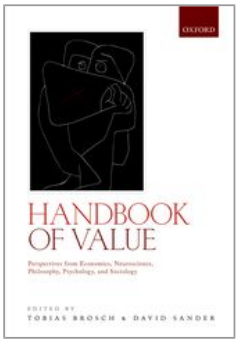

Handbook of Value: Perspectives from Economics, Neuroscience, Philosophy, Psychology and Sociology
Tobias Brosch and David Sander

Print publication date: 2015
Print ISBN-13: 9780198716600
Published to Oxford Scholarship Online: December 2015
DOI: 10.1093/acprof:oso/9780198716600.001.0001

Common value representation—a neuroeconomic perspective

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DOI:10.1093/acprof:oso/9780198716600.003.0005

Abstract and Keywords

How do humans make choices between different types of rewards? Economists have long argued on theoretical grounds that humans typically make these choices “as if” the values of the options they consider have been mapped to a single common scale for comparison. Neuroimaging studies in humans have recently begun to suggest the existence of a small group of specific brain sites that appear to encode the subjective values of different types of rewards on a neural common scale, almost exactly as predicted by theory. This chapter reviews current knowledge about the neural representation of value and choice using human brain imaging studies. It shows that the principle brain area associated with this common representation is a subregion of the ventromedial prefrontal cortex (vmPFC)/orbitofrontal cortex (OFC). The

data available today suggest that this common valuation area is part of a core system that participates in day-to-day decision making suggesting both a neurobiological foundation for standard economic theory and a tool for measuring preferences neurobiologically.

Keywords: neuroeconomics, fMRI, common currency, vmPFC, striatum, value, primary rewards, meta-analysis

> When we talk mathematics, we may be discussing a secondary language built on the primary language of the nervous system.
>
> *As quoted in* John Von Neumann, 1903–57 *(1958) by John C. Oxtoby and B. J. Pettis, p. 128.*

Background

Economics is a wonderful discipline. It is based on clear and precise definitions, axioms, and mathematical formulas. In many cases, economic theory has been successfully used to inform policy, predict human behavior and structure the financial system. In the last 300 years there has been a tremendous advancement in economic theory; from the revolutionary ideas of Daniel Bernoulli, David Ricardo, and Adam Smith through the theories of Vilfredo Pareto, Paul Samuelson, John von Neumann, and Oskar Morgenstern, to the more recent approaches of Herbert Simon, Daniel Kahneman, and Amos Tversky, and many others. However, one of the most fundamental notions in economics is that the basic aim of economic theory is to make predictions. Economists acquire observable behavioral data and through well-defined theories create predictions. What they care about is how well they can predict. As a discipline they are not interested in understanding the underlying mechanisms of *why* the predictions were at a certain level in a given situation. Although they acknowledge that human behavior is a result of neural activity, they remain agnostic to the actual mechanism within the nervous system responsible for those behaviors. Similar to the behaviorism community in psychology in the 1940s, economists in general are not interested in the “black box.”

On the other hand we, as neuroeconomists, are very much interested in the “black box” and we want to understand what is the underlying neural mechanism for the instantiation of value and choice. We strongly believe that taking this approach offers certain advantages. First and foremost, having more data than less is always beneficial in trying to understand any given mechanism. Second, understanding the neural mechanisms of value and choice will set physiological boundaries on any economic theory. A theory that does (p.86) not take into consideration these boundaries will be a priori false, at least at some level of analysis. Moreover, adding these boundaries into the current economic theories will, we believe, make the theories more accurate in their predictions. Third, if the instantiation of all behavior rests in neural activity, then understanding the underlying mechanisms of choice will help us build novel theories that are based not upon arbitrary axioms but natural axioms that are the result of the general and basic physiological principles governing neural activity and hence behavior.

The general neuroeconomic theory of value and choice is only in its infancy, and there are plenty of unknowns. It might even be the case that the general theory will soon be very far from its current form. However, we believe that not pursuing the goal of developing a general theory of value and choice using neural activity (and dismissing its relevance to economics) is both short-sighted and goes against the very spirit of scientific inquiry. Finally, and perhaps most importantly, there can be no doubt that ultimately, a physiologically realistic model of how we make decisions will have better predictive power than an unrealistic one—especially in domains where we have very little behavioral data. This is because models that lack a mechanistic foundation (“non-structural models” in the language of economics) simply cannot outperform models that make novel predictions based on an understanding of underlying mechanism when predicting “out of sample.”

The idea of a common currency representation at a purely theoretical level is, of course, hardly new. The core principal of economic rational choice theories is *utility maximization*, which assumes that choosers act consistently to maximize an internal measure of satisfaction, or utility. By definition, utility

is an ordinal entity having arbitrary units on a unified scale. In theory, this allows one to compare options on the basis of comparing the utilities of the options, which are on a common scale.

The foundation for utility theory can be traced to early work in probability theory, as scholars who sought to reconcile mathematical models of choice and human behavior. Initial work proposed that decisions should be guided by the multiplicative combination of outcome probability and magnitude, or *expected value*. However, such simple models failed to describe how human choosers actually behave, particularly concerning large rewards and small probabilities (i.e., the St. Petersburg paradox). Rather than expected value, which is by definition an objective formulation, Daniel Bernoulli proposed that choosers instead transform *expected value* to an internal *subjective* representation of value, which is a quantity incorporating an individual's subjective aversion to risk (Bernoulli 1738). This notion is very similar to the well-known *Weber–Fechner* transformation of objective sensory stimuli to the subjective perception of the stimuli in psychology.

More recently, a body of mathematical work by Samuelson and others developed the modern axiomatic approach to examining choice behavior (Samuelson 1947). These models revolutionized economics by defining rationality; describing the properties of choices consistent with maximizing an ordered, internal representation of value, termed *utility*. In normative theories of economics, *consistency* is defined by a set of several mathematical axioms, which in essence are testing how consistent an individual is in her choices. Violations of the axioms result in inconsistent or *non-rational* behavior.

(p.87) Why is rational behavior so important to economic normative theories? First and foremost, the economist Paul Samuelson and his colleagues (Samuelson 1947) proved almost a century ago that any decision-maker who is internally consistent in their choices behaves, during the period in which they are consistent, exactly "as if" they were employing a

single fixed common scale for the representation of value. That is, if a chooser is rational, there is at least one utility function (the function that states how the objective value is transformed to internal subjective value representation that guides the choices of that particular individual) that can describe her choices. Second, if a decision-maker demonstrates non-consistent preferences, i.e., behaves in a non-rational way, one could exploit this by taking away money from the non-rational chooser, even when the chooser carefully and precisely makes decisions with full information.[1]

Of course, the assumption that a chooser is consistent is not a necessary condition for a common currency representation.[2] But since Samuelson's proof, nearly all theories of decision, from expected utility theory (Von Neumann and Morgenstern 1944) through prospect theory (Kahneman and Tversky 1979) and even to modern reinforcement learning algorithms (Sutton and Barto 1998) have shared the notion that in order to choose, the different attributes of each option must at some point be converged, however idiosyncratically, incompletely and imperfectly, into a single value for the actual process of comparison.

In this chapter we review current knowledge about the neural representation of value and choice using human brain imaging studies. Although there are ample data and wonderful insights from studies on non-human animals, we focus on human data for the sake of brevity. Throughout this essay we have tried to answer one simple but fundamental question which may inform the general theory of value and choice: Is there evidence for a brain area/neural network that represents value and choice for any given reward type in any situation using a single *common neural currency*?

The main question

At a neurobiological level how does a thirsty animal choose between one or two milliliters of water? How does the human brain choose between one apple or two apples? In principle this seems fairly straightforward. If we assume that "more is better" under these conditions, then we simply need to represent and compare quantities. But what happens in the

brain when we need to choose between a large amount of water and a single apple? Or a small amount of water and two apples? The options we face in these situations are (p.88) different, and our answers depend on the reward types, the quantities of each of those rewards, and our internal metabolic states. So critically: just counting will not help. What we need to do is to take into consideration many different attributes of each option (like color, size, taste, health benefits) and of ourselves (like how hungry or thirsty we are), assess the value of each of the attributes, and combine all of these attributes into one coherent value representation that allows comparison with any other possible option. What we need, at least in principle, is a single (perhaps context dependent) common currency of valuation for comparing options of many different kinds. In as much as our choices are consistent and lawful, the brain must behave as if it represents the values of many different kinds of rewards on a common scale for comparison and choice.

Over the course of the last decade there has been a wealth of studies suggesting that activity in a small number of brain areas encodes reward quantities during decision-making tasks. Areas like the parietal cortex appear to encode how many milliliters of juice an action will yield to a thirsty monkey. Areas like the ventral striatum and the medial prefrontal cortex appear to encode the amount of money an option will yield. Indeed, there is now broad consensus in the neuroscience of decision-making community that reward magnitude is represented in a small number of well-identified areas. In this chapter we will describe some of the main findings supporting the notion that there are a few brain areas that represent various aspects related to valuation and choice. We will focus on evidence from human functional magnetic resonance imaging (fMRI) studies conducted over the last decade, which suggests that one of these reward magnitude encoding areas, the ventromedial prefrontal cortex/orbital frontal cortex (vmPFC/OFC),[3] can be thought of as representing the value of nearly all reward-types on a single common scale that predicts behaviorally observed comparison and choice. Of course, this does not mean that common currency representations occur only in this area, but available

fMRI evidence clearly indicates the existence of a common currency network at least in this area.

Perhaps the first common currency representation experiment was conducted while recoding from monkey parietal cortex (Deaner et al. 2005; Klein et al. 2008) and related work has also indicated that the midbrain dopamine neurons employ a common currency for reward representation in monkeys (Matsumoto and Hikosaka 2009). For the purposes of this review, however, we restrict ourselves to the rapidly growing human fMRI literature on this subject in the frontal cortex so as to focus our analysis on the best understood structural features of the human brain related to this class of representation.

(p.89) Monetary rewards

Over the course of the last decade there have been a huge number of studies that have related the magnitude of monetary rewards, and the idiosyncratic values subjects place on those rewards, to brain activations in humans. In a typical study of this kind, subjects either receive, or choose between, monetary rewards of different sizes during a scanning session. The study then searches for correlations between either the size of the reward or subject's subjective valuations of reward magnitudes and the BOLD signal throughout the brain. Perhaps surprisingly, these studies have yielded a very homogenous result. Essentially all of them identify the medial prefrontal cortex, the ventral striatum, and the posterior cingulate cortex (PCC) as correlated with these reward magnitudes. In addition, a subset of these studies reveal correlations in the amygdala, the insula and the posterior parietal cortex (PPC) (for reviews of this literature see: Grabenhorst and Rolls 2011; Kable and Glimcher 2009; Padoa-Schioppa 2011; Platt and Huettel 2008; Rushworth 2008; Wallis 2011).

Delgado and colleagues (Delgado et al. 2000), for example, used a magnitude evaluation task with monetary rewards to show that activity in the ventral striatum was correlated with monetary gains and losses. Rebecca Elliot and her colleagues, at the same time, showed that ventral striatal activity correlates with the magnitude of cumulative rewards (Elliott

et al. 2000) and Brian Knutson showed, again at essentially the same time, that activity in this area correlates with the anticipation of reward (Knutson et al. 2001). Subsequent studies have clearly supported these early findings; monetary reward expectation (Breiter et al. 2001), monetary reward receipt (Elliott et al. 2003), the expected values of rewards (Knutson et al. 2005), potential monetary reward magnitude and loss magnitude (Tom et al. 2007) and discounted reward value at delays ranging from minutes to months (Kable and Glimcher 2007) are all correlated with activity in the ventral striatum—to cite just a tiny fraction of the relevant literature.

A similar story seems to hold in the medial prefrontal cortex and to a lesser degree in the posterior cingulate cortex. Activity in these areas correlates with monetary reward magnitude (Knutson et al. 2001; Knutson et al. 2003), the expected values of monetary lotteries (Knutson et al. 2005), the subject-specific valuations of gains and losses (Tom et al. 2007), and subject-specific discounted reward value (Kable and Glimcher 2007). To summarize a huge literature, activity in these areas seems extremely well correlated with how good a reward outcome will be and this is true even when the notion of “how good” must incorporate subject-specific subjective evaluations like the tradeoffs between how long one has to wait for a reward and how large is that reward (Kable and Glimcher 2007; McClure et al. 2004).

Primary rewards

It has also been demonstrated that the vmPFC/OFC, striatum and other value-related areas represent value-related signals of primary rewards per se, not the sensory stimuli that are associated with those rewards. For example, O’Doherty and colleagues (O’Doherty et al. 2000) (p.90) demonstrated that activity within the vmPFC/OFC decreased in response to the odor of a food that was eaten to satiety when compared to the response when that food had not yet been consumed (here satiety is an indication of reduced reward value, usually termed *sensory specific satiation*). In another study, O’Doherty and colleagues (O’Doherty et al. 2001) showed that the vmPFC/OFC and the amygdala represent both pleasant and unpleasant tastes, suggesting that these areas code for both positive and negative values as is required for a brain area to

be considered part of a general network representing values for all reward types along the entire subjective scale. Interestingly, in a later study O'Doherty and colleagues (O'Doherty et al. 2002) demonstrated that only the vmPFC/OFC represented both the expectation of reward and actual reward receipt, further strengthening the notion that the vmPFC/OFC represents value on a common scale.

In non-choice tasks, desirable food rewards also produce increased activity in the vmPFC/OFC (Kringelbach et al. 2003) and, as described in the previous paragraph, the actual consumption of palatable foods also results in a greater activation of the vmPFC/OFC (O'Doherty et al. 2002). Administration of pleasant tastes activates this area (O'Doherty et al. 2001; Zald et al. 2002) and meal consumption has been shown to be associated with increased neuronal activity in the vmPFC/OFC (Del Parigi et al. 2002). The striatum has also been shown to respond to the anticipation of primary rewards (O'Doherty et al. 2002), and activity here is correlated with juice preferences (O'Doherty et al. 2006), meal pleasantness ratings (Small et al. 2003), subjective preferences of goods (Knutson et al. 2007), and food craving (Pelchat et al. 2004).

Even the sight of food cues has been shown to activate the vmPFC/OFC and striatum (Goldstone et al. 2009; Killgore et al. 2003; Siep et al. 2009; Simmons et al. 2005). Studies involving choice tasks also demonstrate the involvement of the vmPFC/OFC and striatum in primary reward value coding. Using food items as rewards, the activity in the vmPFC/OFC was correlated with how much a subject was willing to pay (Hare et al. 2009; Plassmann et al. 2007) both for appetitive and aversive objects (Plassmann et al. 2010), reported experienced pleasantness (Plassmann et al. 2008), decision values (Hare et al. 2008), and the subjective value of delayed juice rewards (McClure et al. 2007), while the striatum was correlated with food reward prediction errors (Hare et al. 2008).

Abstract rewards

An immediate question that comes to mind is whether the neural value representations in the value-related brain areas identified using monetary and primary rewards also represent

values for even more abstract non-monetary and non-primary rewards. In the last decade or so it has been shown that almost all studies that have used these kinds of rewards in value-related tasks, revealed the existence of value-related activity in the vmPFC/OFC and to a lesser extent in the striatum, anterior cingulate cortex (ACC), PCC, PPC, lateral intraparietal cortex (LIP), amygdala, and insula (Glimcher 2011; Glimcher et al. 2008).

For example, Kawabata and Zeki (2004) asked subjects to rate paintings as ugly, neutral, or beautiful while lying inside the scanner. They then contrasted the activity measurements obtained during viewing of ugly and beautiful paintings and found higher (p.91) neural activation in the medial prefrontal cortex for the beautiful versus ugly paintings. O'Doherty and colleagues (2003) looked for brain areas that tracked attractiveness ratings of human faces. To do this, they first acquired attractiveness ratings of human faces from an independent group of subjects. They then presented, to a different group of subjects, the most attractive and the least attractive faces, while subjects were inside the scanner conducting an irrelevant task (stating whether the face was male or female). They demonstrated once again that a subregion of the vmPFC/OFC was more active for the attractive faces as compared to the non-attractive faces. Other studies have showed increased activity in the ventral striatum and vmPFC/OFC when subjects actively rate attractive faces as opposed to non-attractive faces from the opposite gender (Cloutier et al. 2008).

In a similar manner, Yue and colleagues (2007) asked subjects to view pictures of various natural scene pictures while inside the fMRI scanner. Subjects had to rate their preferences (on a scale from 1 to 8) regarding each of the environments presented in the pictures. They found that activity in the ventral striatum was stronger for the scenes with a high preference score as compared to the scenes with a low preference score. In yet another related finding, it has been demonstrated that activity in the ventral striatum correlates with the monetary amount that subjects are willing to bid in an auction paradigm when they listen to novel songs inside the

fMRI scanner (Salimpoor et al. 2013). Furthermore, these authors demonstrated increased functional connectivity between the ventral striatum and other value-related areas such as the vmPFC/OFC and amygdala and it has even been shown that the valuation of music (see also Levinson, this volume) evidenced in the ventral striatum is associated with an increase in dopamine in this region (Salimpoor et al. 2011).

In another study, Sharot and colleagues (2009) examined the neural correlates of hedonic value (see also Ellingsen et al., this volume). They asked subjects to estimate how much they thought they would enjoy each of a set of possible vacations, sometime in the future. The authors found increased activity in the caudate nucleus (a nucleus that is part of the striatum) previously associated with reward expectancy (Gottfried et al. 2003; Knutson et al. 2001), when considering more desirable vacations. The left amygdala and pregenual anterior cingulate cortex, both previously shown to be associated with representation of monetary valuation (Glimcher et al. 2008), also showed this relationship.

A very recent study showed that when subjects viewed affective images and reported their level of positive or negatives emotions, the activity in the vmPFC/OFC predicted the experienced emotional value of the affective images (Winecoff et al. 2013). This study nicely demonstrated that the vmPFC/OFC encodes both negative and positive subjective emotional value in a similar manner to monetary or primary rewards. In related studies, it has been shown that activity in the vmPFC/OFC also tracks moral judgments (Greene et al. 2001; Moll et al. 2002; see also Moll et al., 2015).

Hence, abstract valuations, such as attractiveness ratings for faces or scenes, emotional value, or even hedonic values, are all represented within the vmPFC/OFC and striatum. Another interesting study demonstrated that the vmPFC/OFC represented preference ratings of simple moving visual stimuli (Zeki and Stutters 2012). This suggests that the vmPFC/OFC represents values even for very basic low level sensory stimuli and that the (p.92) spectrum of value representations are very broad and general and do not relate only to rewards that we

either consume or from which we derive notable aesthetic or hedonic pleasure.

Bargaining, charitable giving, reciprocal situations, and morality

In the previous sections we have focused on value representations in conditions where the choices an individual had to make were made in isolation and had direct impact only on one's own self. However, in many cases, the choices we make influence other peoples' well-being and other peoples' choices will influence our well-being. The question that arises is whether value representations in both of these cases are located within the same neural value networks, and specifically, is there evidence that the vmPFC/OFC represents values in social and interactive situations?

One of the early studies in this domain came from the work of Sanfey and colleagues (2003b) in which they measured subjects' neural activity while inside the fMRI scanner when they had to decide whether to accept or reject fair and unfair offers in the ultimatum game (UG). They found that the anterior insula correlated with the unfairness of an offer. That is, the more the offer was unfair, the higher the activity within the anterior insula. It was also shown that the activity in the anterior insula could be used to predict subjects' propensity to accept or reject an unfair offer (Sanfey et al. 2003b; Tabibnia et al. 2008). Importantly, the anterior insula has been identified in many other value-related studies as negatively correlated with reward values (for a review see: Levy and Glimcher 2012). It is well known that the anterior insula gets direct inputs from the vicera and is associated with feelings of disgust (Beissner et al. 2013). Hence, it was hypothesized that the feelings of unfair economics offers triggers negative emotions similar to the feelings of disgust.

Subsequent studies have demonstrated that all the main brain areas mentioned in the previous sections that represent the various aspects of valuations as measured in non-social tasks, also represent the various aspects of social-related values such as reward from mutual cooperation, empathy for recipient, aversive response to unreciprocated cooperation, etc. (for a review see: Rilling and Sanfey 2011). For example, it has been shown that reciprocated cooperation in the trust game is

associated with activation in the caudate nucleus, which is part of the striatum (Delgado et al. 2005; Rilling et al. 2002; Rilling et al. 2004) and the vmPFC/OFC (Rilling et al. 2002; Rilling et al. 2004). Importantly, the level of neural activity in the caudate nucleus can even be used to predict the tendency to cooperate (King-Casas et al. 2005; Rilling et al. 2002). We direct readers who are interested in a more in-depth analyses of the neural value representations of social interactions to some excellent reviews (Rilling et al. 2008; Rilling and Sanfey 2011; Ruff and Fehr 2014).

In a similar manner to reciprocal interactions, there are several other human behaviors that also require the ability to prefer others' benefits and increased utility at the expense of one's own benefit. These kinds of behaviors are collectively known either as altruistic behaviors or other-regarding preferences, and in many cases there are driven by moral beliefs. When people engage in these sort of decision problems they must evaluate and compare the costs of giving something away, which could be a material reward, time, or (p.93) even physical work, to the value they derive from the abstract notion of doing something good or preventing something bad from happening to other people or, in some cases, the value derived is in the form of an abstract goal, principle, or belief. The question again is whether there is evidence that the same core valuation areas represent the values of these very abstract and non-materialistic values.

One of the classical paradigms used for examining these kinds of choices is charitable donation. In these kinds of tasks, subjects usually have the option to decide either to donate money to some charitable organization (which would be considered an example of an altruistic or other-regarding behavior) or to keep the money to themselves. Several studies have indeed demonstrated that some parts of the vmPFC/OFC and striatal regions, represent value-related signals while subjects were evaluating and deciding whether or not to donate to a charitable organization or cause (Harbaugh et al. 2007; Moll et al. 2006; Waytz et al. 2012). In yet other related altruistic tasks, similar patterns of activity were observed (Dawes et al. 2012; de Quervain et al. 2004). (For reviews see:

Fehr and Camerer 2007; Forbes and Grafman 2010; Moll et al. 2008.)

Lesions

Lesion studies are an excellent tool to examine the importance of a brain area in given situations and tasks. Lesion studies were amongst the earliest demonstrations of the importance of the vmPFC/OFC in decision-making. It is widely accepted that patients with lesions in the vmPFC/OFC show poor social and individual decision-making skills and abnormal anticipatory emotional responses. The early studies showed that lesioned patients demonstrate abnormalities in their choice behavior, their ability to correctly estimate winning probabilities, or deal with uncertainties (Bechara et al. 1999; Bechara et al. 1997; Rogers et al. 1999), or to solve real-world problems such as financial planning and other problem-types involving planning and look-ahead components (Bechara et al. 1994; Bechara et al. 2000; Goel et al. 1997). Patients with damage to the PFC even show a tendency for riskier decision-making and an apparent disregard for negative consequences of their actions (Rahman et al. 2001).

Later studies also showed that damage to this area leads to difficulties in choosing between options with uncertain outcomes, whether in the form of risk or ambiguity (Camille et al. 2011; Fellows and Farah 2005; Hsu et al. 2005; Manes et al. 2002; Sanfey et al. 2003a; Valentin and O’Doherty 2009), and to difficulties in adjusting responses when the reinforcement value of stimuli change, as demonstrated in impaired reversal learning tasks (Fellows and Farah 2003; Hornak et al. 2004). Lesion studies also demonstrated the crucial role that the vmPFC serves in social valuation. For example, vmPFC-lesioned patients rejected unfair offers more often than controls (Koenigs and Tranel 2007).

A main question that arises from these lesion studies is whether the vmPFC/OFC is necessary for representing values per se or is necessary only when there are choices that involve uncertainty, ambiguity, or the need to update value during a learning task. Two very elegant studies demonstrated that damage to the vmPFC/OFC resulted in less consistent choices during simple preference judgment tasks (Camille et al. 2011;

Fellows and Farah 2007). (p.94) All of these data thus suggest that an intact vmPFC/OFC is crucial for basic value representations and for obeying the fundamental axioms of economic rationality.

It has also been shown that patients with vmPFC/OFC lesions do not report any feelings of regret and they do not anticipate possible negative consequences that might occur as a result of their choices (Bechara 2004). Hence, the data suggest that the vmPFC/OFC is also mediating the role of counterfactual thinking in valuation. That is, it is not just representing values of the actual choices but it is also representing the values of other possible options that we did not take but could have taken (for a review see: Walton et al. 2011). This is an important aspect of learning the values of options in the environment and updating them for future choices.

More than one reward type

However, in all of the studies described above, only a single reward-type and a single task-type were used to examine the neural representation of value. While these studies clearly identified important areas that participate in value representation and choice, they can only provide circumstantial evidence for the notion of a single neural common currency that represents values across reward types. The more direct evidence for this notion that serves as the main claim for this chapter arises from studies that search specifically for a common representation of value across different choice tasks or across different reward types measured within individual subjects.

Different choice tasks within an individual

One of the first studies to use more than one behavioral task to search for the neural representation of a single reward-type, in this case a monetary reward, was a 2009 study by Glascher and colleagues. In that experiment, subjects completed two versions of a monetarily rewarded decision-making task while in an fMRI scanner. In the first version, subjects chose between two different visual stimuli that were associated with two different probabilistic monetary rewards. They hypothesized that under these conditions the visual cues

would come to be associated with monetary values and it was those stimulus-based value representations that they hoped to identify. In the other version, subjects made choices between two different motor responses in the absence of visual cues, each of which was also associated with a probabilistic monetary reward. They hypothesized that under these conditions the motor actions would come to be associated with the monetary rewards and it was the neural representation of these action-values that they hoped to identify. They found that the activity of a subregion of the medial prefrontal cortex—a region that had been identified previously in the single-task and single-reward studies mentioned above—correlated with expected future reward in both task versions.

A closely related paper by Peters and Buchel (2009) searched for brain areas that represent the subjective values of delayed monetary rewards and the subjective values of risky monetary lotteries. Their main finding was, again, that a subregion of the medial prefrontal cortex, which they referred to as the OFC, tracked the subjective value of both (p.95) delayed and probabilistic rewards. They also found that the ventral striatum showed this same pattern of activity. Levy and colleagues (2010), in a similar vein, searched for neural representations of both risky (when the probabilities are known) and ambiguous (when the probabilities are unknown) monetary lotteries. Again they found both of those representations in the medial prefrontal cortex and the ventral striatum. Basten and colleagues (2010) even showed that when subjects must integrate information about both monetary gains (benefit) and monetary losses (cost), activity in this same medial frontal area is correlated with the integrated difference between these two properties. In a related study, Treadway and colleagues (2012) showed that dopamine function (measured using PET) within the vmPFC/OFC and striatum correlated positively across subjects, and the insula correlated negatively with the willingness to invest effort for the opportunity to win larger rewards. This study nicely links the activity within some of the main value-related areas with dopamine function in cost–benefit calculations of values. However, note that Croxson and colleagues (2009) observed that cost–benefit representations of net value was evident in

the striatum and not in the vmPFC/OFC but rather in an adjacent area; the dorsal anterior cingulate cortex (ACC)—an area in which there is significant ongoing inquiry.

Another recent study examined whether value representations of empathic choice, to choose on behalf of others in order to maximize their well-being, is located in the same brain areas that represent values when one chooses for oneself (Janowski et al. 2013). In two separated scanning sessions, subjects made monetary bids for DVDs; either for themselves or for other subjects. In agreement with the studies described above, activity within the vmPFC/OFC correlated with the amount of money the subjects bid for themselves *and for others*. Therefore, this study demonstrates that when we value items or options that do not benefit us directly, we employ similar brain mechanisms and brain areas.

From these studies, and a host of others, it seems clear that a subregion of the vmPFC/OFC appears to encode subjective monetary value signals of almost every kind and it suggests that these different kinds of monetary values may be represented on a common scale, irrespective of task details. But much more compelling evidence of a common currency for reward comparison would be the demonstration that, within an individual, value representations for fundamentally different reward types arise in exactly the same areas.

Multiple reward types in the same task

FitzGerald and colleagues (2009) were the first to conduct such a study. They searched for value-related representations of money and consumer goods like mugs, boxes of chocolate, and universal serial bus (USB) keys. Subjects had to choose between receiving (or giving up) some amount of money and receiving (or giving up) a few of these consumer goods. The authors found that activation in the vmPFC/OFC (and also in the PCC, and the insula—which showed a negative correlation) was correlated with the difference between the subjective values of the two available options. Importantly, they showed that this was true for both gains and losses. Soon afterwards, Chib and colleagues (2009) made this argument in a more fundamental way when they explored the neural representation of three different reward types using a within-

subject design. They explored the value-associated (p.96) representation of money, snack foods, and CalTech novelty items like hats (trinkets) in single individuals. Their design was organized into two scanning sessions. In the first, subjects chose on each trial between a certain monetary gain and a probability of winning a snack food or trinket. In the second session these same kinds of choices were made, but this time between the certain win of a fixed snack food and probability of winning a trinket or a given amount of money. Once again, they found that a subregion in the vmPFC/OFC represented the subjective values of all three reward types.

Ishizu and Zeki (2011) examined whether the experience of perceiving beauty derived from different sources would result in similar neural value representations. In their study, subjects rated how beautiful both auditory and visual stimuli were while inside the fMRI scanner. The auditory stimuli were classical and modern excerpts of music and the visual stimuli were paintings. The authors found a subregion within the vmPFC/OFC that tracked value ratings of both auditory and visual stimuli, suggesting that activity within the vmPFC/OFC tracks subjective valuation not just for different reward types but also for the valuation of sensory events that originate from different sensory modalities.

In line with these studies, Kim and colleagues (2011) examined brain activity while subjects made a forced choice between visual cues associated with positive/negative amounts of money and appetitive/aversive fluids delivered orally while in the scanner. They found that a subregion of the vmPFC/OFC tracked the expectation of receiving both monetary and fluid offers—showing increasing BOLD activity for positively valued fluids and monetary events and decreasing activity when either of those was of negative value. Interestingly, they also found that the right anterior insula had a negative correlation with increasing expected reward value for both money and juice. Another study demonstrated that neural activity within the dorsal striatum represented a value-teaching signal (a *reward prediction error*) while subjects learned the values of monetary and juice rewards (Valentin and O’Doherty 2009).

Talmi and colleagues (2009), in yet another related study, examined the interaction between monetary rewards and physical pain. Subjects in that study chose between two stimuli, each associated with either a high or low probability (75 and 25 per cent, respectively) of earning money and a high or low probability of experiencing pain (thus creating a 2×2 stimulus design). Thus when subjects faced a possible monetary gain they had to take into consideration the “cost” of receiving possible pain when making their choices. What the authors found was that the cost–benefit value signals converged in an interactive manner: Activity in the insula was correlated with the behavioral impact of the pain on their choices, and this insula activation was inversely correlated with activity in the vmPFC/OFC. The greater the perceived cost of the pain, the lower the activity in the vmPFC/OFC, and this effect appeared to be modulated through the level of activity in the insular region they examined. Another study also examined how humans integrate the value of monetary rewards and physical pain (Park et al. 2011). In that study subjects had to decide whether to accept or reject offers that were combinations of some amount of money and some amount of physical pain (low current electrical stimulation applied to the finger) while lying inside the fMRI scanner. Again, the authors found that the activity within the (p.97) vmPFC/OFC correlated with the subjective values of the combined monetary and pain rewards.

Izuma and colleagues (2008) expanded the domain of reward studies of this kind when they examined the neural representation of both social and monetary rewards. In their experiment, subjects engaged in a monetary task and a social reputation task. Acquiring positive reputation and gaining monetary rewards both activated the same area in the left striatum, suggesting that monetary rewards and social rewards are represented in a similar manner in the striatum. Lin and colleagues (2012) also examined the interaction between monetary and social values in a probabilistic choice task. On some trials, subjects had to choose between two uncertain social rewards and on other trials between two uncertain monetary rewards. Again, they found that activity in

a subregion of the vmPFC/OFC correlated with both monetary and social subjective values.

In many decision-making studies of this kind, however, the choices subjects make are hypothetical and do not result in real payment. This is a source of some concern, particularly in the economic community. For many scholars it is important to examine the neural mechanism for representing gains and losses when subjects are conducting a choice task using hypothetical rewards and when they are using real rewards. Fortunately, Min Jeong Kang and colleagues (2011) examined these questions while subjects earned both real and hypothetical rewards inside the fMRI scanner. They found that subregions of the ventral striatum and the vmPFC/OFC tracked the value of various goods in both real and hypothetical choice conditions.

Common currency representation

These studies all suggest that the vmPFC/OFC, and perhaps the ventral striatum, represent the values of rewards of many different, and perhaps all, kinds. But in order to demonstrate that these representations exist in a single common currency appropriate for computing the tradeoffs that guide choice, one must also show that the activity level in these areas is equivalent whenever subjects report that offers of two different kinds of rewards are equally desirable. There are two papers that have done that, finding that equal behavioral value equates to equal BOLD signal in the vmPFC/OFC; evidence for a neural *common currency*. The BOLD signal, however, is not actually a direct measure of neural activity but rather a measure of the metabolic demand, and thus only a proxy for the actual neural activity (Huettel et al. 2008). Thus while our current understanding of fMRI strongly indicate the existence of neural activity encoding value in a common currency, the final proof that neural activity encodes value on a common scale will ultimately have to be made electrophysiologically (and to some degree already has been made in monkeys; Deaner et al. 2005). With that important caveat, we turn to those two studies.

The first study to provide evidence for a common currency representation in the BOLD signal was by Smith and colleagues (2010). In that study, male subjects performed two tasks while being brain scanned: A forced-choice task in which subjects could either win or lose money while watching female faces that ranged from very attractive to very unattractive, (p.98) and a second task in which subjects had to decide how much money they were willing to spend to view a female face at a given level of attractiveness. This allowed them to establish an explicit exchange rate between viewing female faces and money, and then to scan face/money combinations, thus establishing a common neural representation of value for both reward types. They found that a specific subregion in the anterior parts of the vmPFC/OFC tracked the subject-specific values for each of the reward types. More importantly though, they found a subregion in the posterior part of the vmPFC/OFC that predicted the exchange rate between money and faces, established in the second task, across subjects. This is important because their data suggest that this particular area tracks the subject-specific values of faces and money in a single common neural currency.

The second study that used this strategy came from our labs (Levy and Glimcher 2011). We had very similar results using a different task that examined the neural representation of the value of food items and money. In that study, hungry subjects made choices between certain and risky rewards of money or foods (either chocolate M&Ms or Ritz crackers) inside the fMRI scanner. Out of the scanner we also had subjects make choices between fixed monetary offers and probabilistic lotteries over foods in order to establish the exchange rate between food and money for each subject. From this paradigm we were able to identify, as have the many previous studies mentioned above, that subregions of the vmPFC/OFC and the striatum tracked the subjective values for both money and food. We then asked whether the activation levels of these subregions that tracked the values of both food and money could be used to predict the exchange rate for food and money identified behaviorally outside of the scanner. Our data indicated that in the vmPFC/OFC region that represented both

reward types, activity levels predict the exchange rate between money and food.

A third recent study also merits discussion in this regard, although it employed a different strategy to answer the same question of whether we can find strong evidence for a common currency representation in the vmPFC/OFC (McNamee et al. 2013). Similar to the Chib and colleagues (2009) study, the authors of this study first measured subjects' willingness to pay for three different reward types (money, snack foods, and trinkets) while inside the fMRI scanner. However, instead of only employing a standard univariate analysis, they used a multi-voxel pattern analyses method (for a review of this method, see: Haynes and Rees 2006; Norman et al. 2006) to relate neural activity to subjects' willingness-to-pay. First, they looked for subregions within the vmPFC/OFC that specifically tracked the value of only one reward-type, which they termed category-dependent value signals. For this, they developed an algorithm that searched for voxels encoding one stimulus category only and then determined if activity in these same voxels could be used to decode the value of independent items from that same category and *not* items from other categories. Second, they looked for subregions within the vmPFC/OFC that tracked values irrespective of reward type, which they termed category-independent value signals. They found subregions in the more ventral parts of the vmPFC/OFC representing category-dependent values (but only for food and trinkets). More importantly, they found a more dorsal area of the vmPFC/OFC (in an area that is closely related to those found in the (p.99) previous overlapping studies described in the previous sections) a category-independent value representation (McNamee et al. 2013). This is a finding that, again, strengthens the notion that there is a subregion within the vmPFC/OFC that represents values on a common currency irrespective of the reward type.

From these studies we can conclude a few things. First, there is compelling evidence that a subregion of the vmPFC/OFC represents the subject-specific subjective value of multiple reward-types, across various tasks, and in a common neural currency appropriate for guiding choice. Second, there is

some evidence—although this is much less certain—that suggests the insula may also represent subjective value in a common currency under some conditions, but in a negative manner, and finally there is evidence that the striatum may also represent subjective value.

Conclusions about the striatal representation are complicated by two factors. First, single-unit studies in the monkey (Lau and Glimcher 2008; Samejima et al. 2005) report a robust subjective value signal in the dorsal striatum, which has rarely been observed in human fMRI. This disparity may be due to the fact that the value-encoding neurons in the dorsal striatum are diffusely distributed (Kawagoe et al. 1998; Lau and Glimcher 2008) and thus difficult to image using fMRI. Using fMRI, however, value-related signals have been very widely observed in the ventral striatum (see references throughout this chapter), an observation, which has only begun to be confirmed with single unit recording methods.

Meta-analyses

When we last reviewed studies of value representation and choice (Kable and Glimcher 2009) there was a tremendous amount of evidence suggesting that the vmPFC/OFC region played a critical role. Literally dozens of studies available at that time pointed toward this area as critical. Since that time, not only have many other single-reward studies continued to point toward that area as critical, but a host of fMRI studies have now converged on the vmPFC/OFC as the site of a common neural currency for value representations. With all of this apparent convergence it seems important to ask whether it is really the same area that is active in these many studies by many different labs. Put another way, how strong is the evidence for an anatomically localized subregion in the human frontal cortex that tracks subjective values on a common currency for all previously studied reward-types?

In order to answer this question we and others have conducted meta-analytic studies. In our meta-analysis (Levy and Glimcher 2012) we used data from thirteen principle studies that used more than one reward-type and/or one task. We took the coordinates specified in those studies of the voxel

that was most active (peak voxel) for the value-related signals measured (mainly based on conjunction analyses between reward types or tasks). We marked these coordinates on a single brain template (using Montreal Neurological Institute coordinates). As can be seen very clearly in Fig. 5.1, the coordinates describing the peak voxels are in the vmPFC/OFC and in nearly all of these studies are strikingly similar.

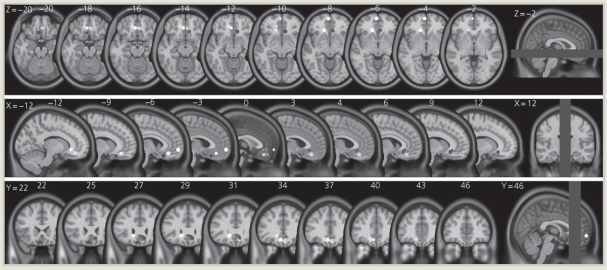

Fig. 5.1 Peak voxels in the subregion of the vmPFC/OFC representing value-related signals from thirteen studies that used more than one reward type and/or one task as described in (Levy and Glimcher 2012). The coordinates of the peak voxels were taken from the original studies and are detailed in Levy and Glimcher (2012). Brain images are the T1 MNI-152 template. (See Plate 2.)

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The other meta-analyses have come to very similar conclusions. Bartra and colleagues (2013) conducted a meta-analysis on 206 value-related fMRI studies. As can be seen in (p.100) (p.101) Fig. 5.2, they found that across all studies and irrespective of the reward type used, activity in the vmPFC/OFC, the PCC, and the anterior-ventral striatum were positively correlated with subjective value. They also found that the dorsal and posterior striatum (a different part than the striatal area associated with the common unified system), thalamus, anterior insula, and the dorsomedial PFC, have a quadratic relationship with value as opposed to the more linear positive correlation observed in the general value-related brain areas. They suggested that the quadratic pattern probably represent an arousal or a salience signal, while the linear relationship found in the vmPFC/OFC, PCC, and ventral striatum is indicative of a general unified value-related system.

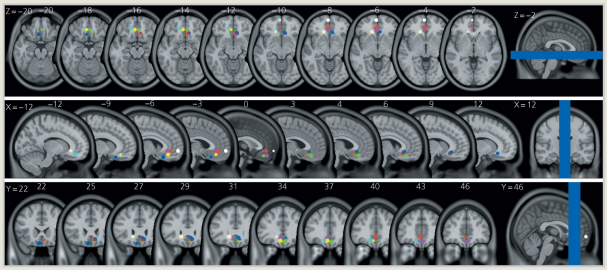

Plate 2 Peak voxels in the subregion of the vmPFC/OFC representing value-related signals from thirteen studies that used more than one reward type and/or one task as described in (Levy and Glimcher 2012). The coordinates of the peak voxels were taken from the original studies and are detailed in Levy and Glimcher (2012). Brain images are the T1 MNI-152 template. (See Fig. 5.1.)

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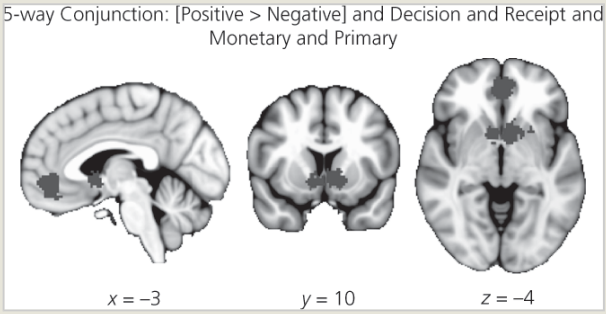

Fig. 5.2 A five-way conjunction analysis, designed to identify brain areas that represent subjective value irrespective of reward type. The conjunction analysis was conducted on voxels that showed significantly greater density for positive than negative effects, and showed high activity for positive events at both the decision and receipt stages, as well as for both monetary and primary reward types. (See Plate 3.)

Reprinted from *NeuroImage*, Volume 76, 1 August 2013, pp. 412–427, Bartra, O., McGuire, J. T., and Kable, J. W. The valuation system: a coordinate-based meta-analysis of BOLD fMRI experiments examining neural correlates of subjective value, (2013) with permission from Elsevier.

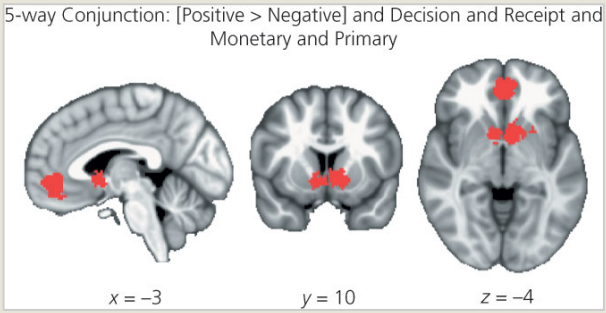

Plate 3 A five-way conjunction analysis, designed to identify brain areas that represent subjective value irrespective of reward type. The conjunction analysis was conducted on voxels that showed significantly greater density for positive than negative effects, and showed high activity for positive events at both the decision and receipt stages, as well as for both monetary and primary reward types. (See Fig. 5.2.)

Reprinted from *NeuroImage*, Volume 76, 1 August 2013, pp. 412–427, Bartra, O., McGuire, J. T., and Kable, J. W. The valuation system: a coordinate-based meta-analysis of BOLD fMRI experiments examining neural correlates of subjective value, (2013) with permission from Elsevier.

Sescousse and colleagues (2013) conducted an activation likelihood estimation meta-analysis on eighty-seven fMRI studies that examined monetary, primary, and erotic rewards. They came to very similar conclusions: that the vmPFC/OFC, anterior insula, and striatum represent subjective values irrespective of reward type. Interestingly they also identified the amygdala and medio-dorsal thalamus as part of this value network. In a similar manner, Peters and Buchel (2010) demonstrated in a meta-analysis that the vmPFC/OFC area represents various value types such as outcome values, goal values, and decision values. Interestingly, another meta-analysis demonstrated that the vmPFC/OFC and ventral striatum probably do not represent identical value-related signals (Diekhof et al. 2012). They showed that the vmPFC/OFC area was more active during reward outcome, while the ventral striatum was more active

during reward anticipation, strengthening the notion of the striatum's role in value learning and expectations.

In the most recent study of this kind, Clithero and Rangel (2013) conducted a meta-analysis on eighty-one different studies and replicated the results from the previous (p.102) meta-analytic studies. That is, they showed that the vmPFC/OFC, ventral striatum, and PCC are representing various aspects of subjective values across a wide range of tasks, reward types, and choice stages. However, they extended the previous findings by showing that there are several networks that were co-activated with subareas within the vmPFC/OFC suggesting a possible parcellation of information; although questions remain about what exact information is represented within each subnetwork, and how it contributes to the global value signal. Finally the authors found some evidence that suggests a posterior-to-anterior gradient of value representations within the vmPFC/OFC. That is, the more abstract a reward is, the more anterior would be its neural value representation within the vmPFC/OFC.

This strengthens the main conclusion we hoped to convey in this chapter, that the vmPFC/OFC and striatum are principal nodes of one general and unified value-based neural system and that there is a small subregion in the vmPFC/OFC that tracks subjective value on a common currency appropriate for guiding choices between different kinds of rewards. Indeed, these data seem to suggest that the subregions within the vmPFC/OFC and striatum can be used as a basis for constructing an unbiased region of interest (ROI) for further studies of reward and valuation. Because there is now ample data demonstrating that areas in the vmPFC/OFC and striatum correlate with value signals, it now seems appropriate to conclude that research can begin to advance from using whole-brain analyses of fMRI data to a more focused approach reminiscent of the strategy used in electrophysiological studies. This could lead to more concrete and testable predictions, rather than relying on whole-brain analyses aimed only at the cerebral localization of value. The data suggest, in essence, that fMRI studies of value have now advanced beyond the point of whole-brain analyses driven only toward cerebral

localization and to a point where the high-resolution physiology of valuation can become a tractable goal.

Predictions

In fact, several human fMRI studies have now employed this more focused approach and directly used neural activity in specific value-related areas of human subjects to try and predict future choices. Lebreton and colleagues (2009) extracted the neural activity from the vmPFC/OFC, striatum, hippocampus, and PCC while subjects rated how pleasant different reward types were, such as faces, houses, and paintings. They then used these neural activations to successfully predict subjects' preferences for these reward-types as measured in a binary choice task outside the scanner. The most interesting part of that study was that they were able to predict subjects' preferences, even when subjects conducted the binary choice task a month after the fMRI session. This suggests that it is possible to use neural activations from the common value areas to successfully predict subjects' subsequent choices and that these neural activations can be, in some situations, stable enough to make predictions regarding choices made relatively far in the future.

In a subsequent study, Anita Tusche and colleagues (2010) used multi-voxel pattern analysis to determine whether they could predict subjects' subsequent propensity to (hypothetically) buy cars by analyzing subjects' brain activity while they were watching the same (p.103) cars inside the scanner. Interestingly, in that study there were two experimental groups. Subjects in the first group (high-attention group) were requested to consciously attend the cars and to think how much they liked the car they were currently reviewing and to report their answer on a four-point scale. Subjects in the second group (low-attention group) were asked to perform a demanding fixation task. The task was intended to distract subjects from consciously paying attention to the cars, which they did not have to consciously evaluate. After scanning, subjects from both groups were requested to imagine that they were in a store and had to choose a new car. They were shown each of the cars presented before in the scanner and were asked to answer "No/Not sure/Yes" to the

question: “Would you buy this car?” The important thing to note here is that subjects did not know during scanning that they would be asked this question during the second phase outside the scanner. The authors successfully used activation in the insula and in the vmPFC/OFC in order to decode subjects’ subsequent choices. An interesting part of this study was that the authors could predict subsequent choices in both experimental groups. This suggests that value representations within the vmPFC/OFC and other value-related areas are present even when subjects do not consciously evaluate an item. This suggests that valuation is an ongoing non-stop mechanism that operates always and is not dependent on conscious awareness or on attention (although it might be modulated and affected by them).

In a related study, Levy and colleagues (2011) measured the neural activations in the vmPFC and striatum while subjects passively viewed twenty different goods inside the scanner. Thereafter, outside the scanner, they conducted a binary choice task for all possible pairwise comparisons of the same twenty items. From the choices, they constructed an ordinal preference ranking of the twenty items. They then used the measured neural activations to successfully predict subjects’ subsequent choices. Importantly, the authors also constructed an ordinal neural ranking of the twenty items and showed that the two ordinal rankings (behavioral and neural) were significantly correlated across subjects and that the prediction accuracy was a function of the neural ordinal distance. That is, the greater the “neural distance,” the better the prediction power (the maximum accuracy in this study was 82–83 percent). First, this study demonstrated again that one could use the neural activations from the common value areas to predict choice. Second, it demonstrated that the same brain areas are representing value during active choice and during passive evaluation of goods.

Quite a few studies have thus now demonstrated that a subregion of the vmPFC/OFC represents subject-specific reward value in a common neural currency, the *expected subjective value* of neuroeconomic theory (Glimcher 2011). This remarkably small area in both right and left vmPFC/OFC is activated in a way that parametrically correlates with the

subjective values subjects attribute to nearly every kind of reward that has ever been studied in the scanner. The data indicate that when two disparate kinds of rewards are equally desirable to a subject, then activity in this area will be of equal magnitude for these two rewards in that individual. This is strong evidence supporting the claim that a subregion in the vmPFC/OFC tracks subjective value in a single common currency of the kind first described by economic theory hundreds of years ago. Using the insights from all the (p.104) reviewed studies in this chapter we have previously generated a diagram (Levy and Glimcher 2012) that is a suggested possible schema for understanding the decision-making networks of the human brain (Fig. 5.3).

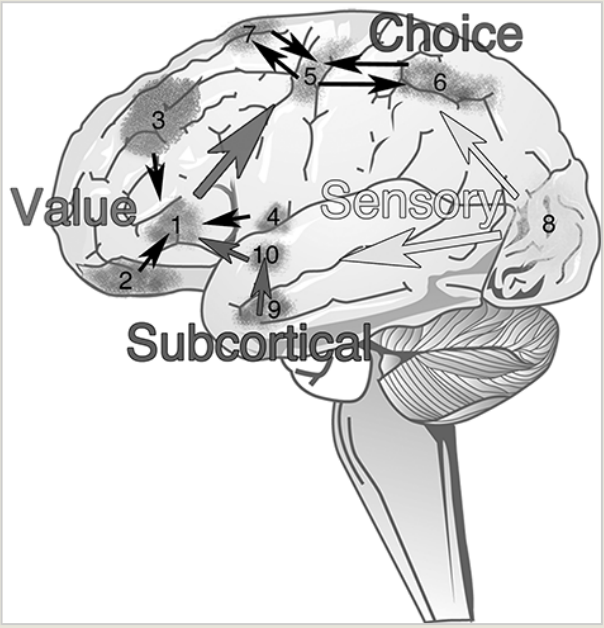

Fig. 5.3 One possible schema for understanding the decision-making networks of the human brain. Current evidence suggests that information from cortical and subcortical structures converges toward a single common value representation before passing on to the choice-related motor control circuitry. Modulatory inputs play a critical role in establishing this final common representation with those inputs carrying signals related to arousal, internal state (satiety, thirst, hormonal levels, etc.) and emotional intensity. In this schema, sensory information from all modalities carries, among other things, the identity and location of the options. We use visual signals in this diagram to stand for information from all sensory modalities. (1) vmPFC, (2) OFC, (3) DLPFC, (4) insula, (5) primary motor cortex (M1), (6) posterior parietal cortex, (7) frontal eye fields, (8) visual cortex, (9) amygdala, (10) striatum. (See Plate 4.)

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A recent study provided supporting evidence for this possible schema (Lim et al. 2013). In that study, subjects had to evaluate T-shirts that varied in their visual esthetic, by varying color or font type and in semantic meaning (the meaning of the logo on a printed T-shirt). Subjects had to rate how much they liked the esthetic appearance of the logo words on the T-shirt, and in another rating how much they liked the semantic meaning of the words. The authors

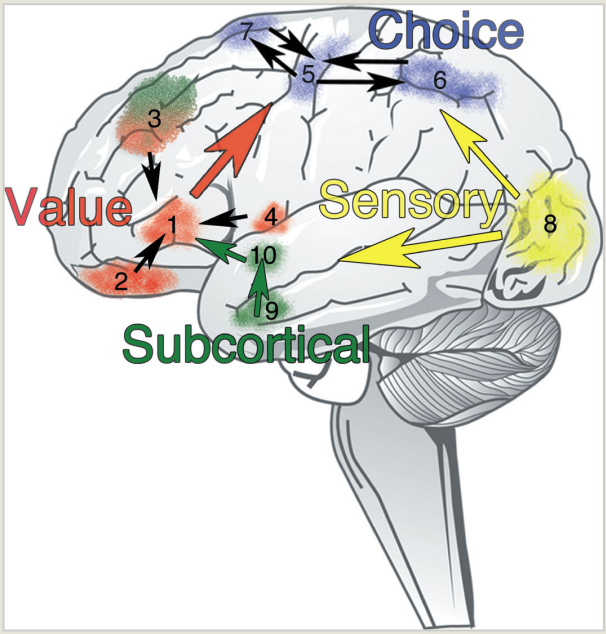

Plate 4 One possible schema for understanding the decision-making networks of the human brain. Current evidence suggests that information from cortical and subcortical structures converges toward a single common value representation before passing on to the choice-related motor control circuitry. Modulatory inputs play a critical role in establishing this final common representation with those inputs carrying signals related to arousal, internal state (satiety, thirst, hormonal levels, etc.) and emotional intensity. In this schema, sensory information from all modalities carries, among other things, the identity and location of the options. We use visual signals in this diagram to stand for information from all sensory modalities. (1) vmPFC, (2) OFC, (3) DLPFC, (4) insula, (5) primary motor cortex (M1), (6) posterior parietal cortex, (7) frontal eye fields, (8) visual cortex, (9) amygdala, (10) striatum. (See Fig. 5.3.)

found that activity in the fusiform gyrus, an area associated with the processing of visual features, correlated with the value of the visual esthetic attributes, but not with the value of the semantic attributes. In contrast, activity in posterior superior temporal gyrus, an area associated with the processing of semantic meaning, exhibited the opposite pattern. Interestingly, they also found that both areas exhibited functional connectivity with a subregion of the vmPFC/OFC that tracked the overall stimulus values at the time of decision. This study again supports the notion that some of the different attributes related to a given item are represented in different and specific brain areas but (p.105) that the neural information of these attributes converge into the vmPFC/OFC (probably to other areas as well) to form a general and combined value representation of a given good.

It is important to note, however, that there is no evidence to support the claim that the neural common currency of value arises only in this subregion of the vmPFC/OFC. Any common currency observed in the brain must reflect the activation of multiple brain areas. It is almost certainly the case that other local and network activations lie beneath the resolution of the techniques used in these studies. Indeed, the evidence reviewed here suggests that portions of the striatum, the PCC, and perhaps the insula also participate in this process.

Another very relevant brain area that is hypothesized to be part of the valuation network is the ACC. First, it has strong anatomical connections with the vmPFC/OFC and other cortical and subcortical areas (Rushworth et al. 2011). Second, it has been shown that the ACC is monitoring several aspects of valuation and choice. It has been shown that it tracks erroneous choices (Rushworth et al. 2004; van Veen and Carter 2002), that it uses current and long-term reward

information to guide appropriate choices (Boorman et al. 2013; Kolling et al. 2014), cost–benefit representations of net value (Croxson et al. 2009), and that it is coding the difficulty posed by conflict between competing choices (Botvinick 2007; Botvinick et al. 2001; Pochon et al. 2008; Shenhav et al. 2014). It is beyond the scope of this chapter to fully describe and discuss the different possible roles that the ACC might have in the common valuation network. We also want to note that the ACC is not a homogeneous area and it could be split into several smaller subregions that subserve somewhat different aspects of valuation (Beckmann et al. 2009; Torta and Cauda 2011). All we want to emphasize here is that it is probably an important part of the common valuation network. We guide the readers for several excellent reviews discussing the role of the ACC in valuation and choice (Noonan et al. 2011; Rushworth et al. 2011; Rushworth et al. 2012; Vassena et al. 2014).

Conclusion

An important point that needs to be considered is that the vmPFC/OFC has long been associated with functions other than decision-related valuation (Schoenbaum et al. 2011; Viskontas et al. 2007; Zald and Andreotti 2011). Factors ranging from emotion (Bechara 2004; Diekhof et al. 2011; Mitchell 2011; Sabatinelli et al. 2011), to social behavior (Viskontas et al. 2007), learning and memory (Corcoran and Quirk 2007; Gilboa 2004; Nieuwenhuis and Takashima 2011; Petrides 2007), through mental disorders such as depression (Lorenzetti et al. 2009; Pizzagalli 2011), post-traumatic stress disorder (Koenigs and Grafman 2009), obsessive–compulsive disorder (Del Casale et al. 2011; Zald and Kim 1996a, b), and psychopathy (Blair 2004, 2010) have all been identified in this brain region. This general area has also been associated with theory of mind (Abu-Akel and Shamay-Tsoory 2011; Lewis et al. 2011; Sebastian et al. 2012) and with the default network (Buckner et al. 2008). Given this host of functional associations, how should one interpret the wealth of data linking a subregion in this area to a function as specific as encoding a common neural currency for decision-making? Of course it is the case that the vmPFC/OFC is a fairly large area

and not all of these functions will be mapped to the precise subregion we identify (p.106) here, but there is enough overlap that this problem cannot be overlooked. And thus the observed overlap of these functions raises the fundamental question of whether we can consolidate all these functions into a unified theory of what this brain area is doing.

An excellent meta-analytic study and review paper tried to address exactly this question (Roy et al. 2012). In that paper, the authors conducted a meta-analysis of thousands of imaging studies using Neurosynth (www.neurosynth.org), which enables one to examine neural activations based on terms frequently used in manuscripts. They examined the relationship between the activation maps of various domains such as memory and “default mode” function, self-reflection, social cognition and mentalizing, emotion, reward, and autonomic and endocrine changes. They found a striking overlap for all these “meaning-related” constructs in the vmPFC/OFC, very similar to the area identified in value-related meta-analyses described in this chapter (see Fig. 5.4). They then conducted a factor analysis of all the various construct-maps they have identified and found two main subsystems that only overlapped in the vmPFC/OFC. They suggested that one system could be termed the “affect generation” system and the other system could be termed the “simulation system.” Interestingly, they also suggested that, based on both these functional subsystems and on anatomical connectivity analyses, the vmPFC/OFC region is a unique area that integrates high-level cognitive signals with signals involved in the most basic forms of affective experience and physiological regulation.

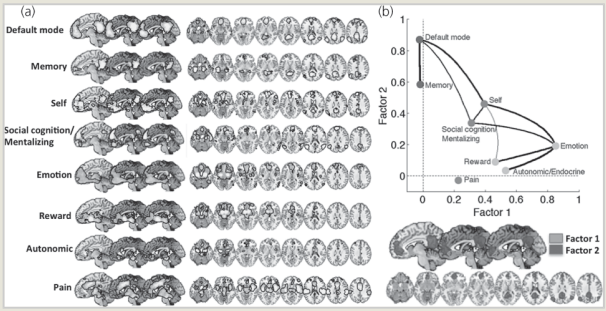

Fig. 5.4 The authors conducted a meta-analysis across various domains ranging from the default mode to reward and pain (see panel (a) for specific domains). They then conducted a factor analysis (with two main factors) across all the functional maps identified for the individual domains. Note that there is an overlap of both factors in the vmPFC/OFC area. For full details please refer to the original manuscript (Roy et al., 2012). (See Plate 5.)

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(p.107) We quote their conclusion of what they suggest as the main common role of the vmPFC/OFC: “. . . the functional role of the vmPFC is not reducible to any one of these functional categories [mentioned in the previous paragraph]. Rather, it serves as a hub that connects systems involved in episodic memory,

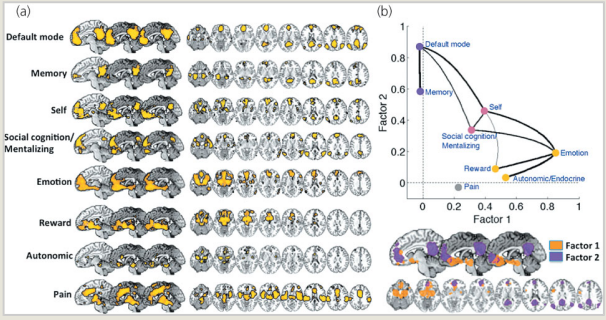

Plate 5 The authors conducted a meta-analysis across various domains ranging from the default mode to reward and pain (see panel (a) for specific domains). They then conducted a factor analysis (with two main factors) across all the functional maps identified for the individual domains. Note that there is an overlap of both factors in the vmPFC/OFC area. For full details please refer to the original manuscript (Roy et al., 2012). (See Fig. 5.4.)

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representation of the affective qualities of sensory events, social cognition, interoceptive signals, and evolutionarily conserved affective physiological and behavioral responses. As such, it plays a unique role in representing conceptual information relevant for survival and in transducing concepts into affective behavioral and physiological responses.” They termed this process or role of the vmPFC/OFC “affective meaning.” They continue and explain that: “. . . meaning centered view of vmPFC predicts that vmPFC and its subcortical connections are not essential for simple forms of affect, valuation, and affective learning, but are essential

when conceptual information drives affective physiological and behavioral responses.” They conclude that the vmPFC/OFC may be considered as a system of systems that integrates signals from many other systems to generate an affective meaning of a situation.

One possibility is that this brain area is associated with many functions in different contexts and states. This possibility, although appealing, does not describe a fundamental and parsimonious principal of how the brain works. One might also hypothesize that a unifying feature of this area might be the notion that this area is representing some kind of value-related signal in each of these contexts. Presumably, what drives and directs much neural activity and subsequent behavior is value maximization in some form and it may be that this is one of several common threads relating the many findings in this brain region.

To resolve these issues more detailed anatomical measurements will be required that can map subregions to specific loci in the brain, ideally at a within-subject level. Given that higher anatomical resolution studies, and studies with causal methods, will be required to relate activation in these brain areas to specific functions any reconciliation would be purely speculative at this stage. The BOLD signal in a subregion of the vmPFC/OFC clearly represents the values of choice objects on a single common neural scale appropriate for guiding choice behavior. What that means for a larger functional assessment of the vmPFC/OFC area remains to be determined. Another open question is: What is the exact functional role in valuation and choice of each subregion within the vmPFC/OFC, based on the specific cytoarchitectonic organization and anatomical connections with other cortical and non-cortical areas? As described above, a recent meta-analysis addressed this question and has suggested some interesting hypotheses (Clithero and Rangel 2013).

Neuroeconomic and decision-making studies in the last decade have revealed some basic notions about the neural circuitry with which we make choices and represent value in our brains. There have been great advances in our understanding

of how we learn and store new values in the brain and how these values influence our expectations and future behavior. In this exciting time, scientists from many fields are working to develop a unified theory of value and choice. This fast-growing area of inquiry will help us not just understand some of the basic principles of how the brain works, but should also help us understand and treat pathologies of choice such as addiction, pathological gambling and obesity.

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Notes:

([1]) Imagine that a chooser prefers apples to oranges, oranges over pears *but* pears over apples, i.e., demonstrating non-consistent preferences. If that person had a pear and we

offered to sell her an orange for her pear plus one cent. She accepts. We then offer her an apple for the orange we just sold her plus one more cent. According to her preferences, she accepts. Then we offer to sell her back her original pear for the apple plus one more cent. She accepts. At the end of these trades she has lost three cents, has her original pear in hand, and considers each trade as a good trade.

([2]) Although under some conditions it may be necessary for a fixed monotonic common currency representation (e.g., (Houthakker 1950).

([3]) Throughout the chapter we use the combined term vmPFC/OFC rather then either of the brain areas separately because there is some inconsistency in the literature regarding what are the authors' anatomical definitions of the vmPFC and/or OFC. In general, we refer to this single area with this combined acronym to highlight the generality of findings across hundreds of studies and to emphasize the importance of this brain area. Most of the studies reviewed in this chapter refer to either the vmPFC or OFC if the activity identified is mainly within Brodmann areas 11, 10, 13, 14, and in some cases 32 (for anatomical reviews see: Ongur et al. 2003; Ongur and Price 2000; Price and Drevets 2010). An anatomical plot of the area we are discussing can be found in two closely related meta-studies (Bartra et al. 2013; Levy and Glimcher 2012).