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# Neurobiology of Economic Choice: A Good-Based Model

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neuroeconomics, subjective value, action value, orbitofrontal cortex,  
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## Abstract

Traditionally the object of economic theory and experimental psychology, economic choice recently became a lively research focus in systems neuroscience. Here I summarize the emerging results and propose a unifying model of how economic choice might function at the neural level. Economic choice entails comparing options that vary on multiple dimensions. Hence, while choosing, individuals integrate different determinants into a subjective value; decisions are then made by comparing values. According to the good-based model, the values of different goods are computed independently of one another, which implies transitivity. Values are not learned as such, but rather computed at the time of choice. Most importantly, values are compared within the space of goods, independent of the sensorimotor contingencies of choice. Evidence from neurophysiology, imaging, and lesion studies indicates that abstract representations of value exist in the orbitofrontal and ventromedial prefrontal cortices. The computation and comparison of values may thus take place within these regions.

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## INTRODUCTION

Economic choice can be defined as the behavior observed when individuals make choices based solely on subjective preferences. Since at least the seventeenth century, this behavior has been the central interest of economic theory (which justifies the term economic choice) and also a frequent area of research in experimental psychology. In the past decade, however, economic choice has attracted substantial interest in neuroscience for at least three reasons. First, economic choice is an intrinsically fascinating topic, intimately related to deep philosophical questions such as free will and moral behavior. Second, over many generations, economists and psychologists accumulated a rich body of knowledge, identifying concepts and quantitative relationships that describe economic choice. In fact, economic choice is a rare case of high cognitive function for which such a

formal and established behavioral description exists. This rich “psychophysics” can now be used to both guide and constrain research in neuroscience. Third, economic choice is directly relevant to a constellation of mental and neurological disorders, including frontotemporal dementia, obsessive-compulsive disorder, and drug addiction. These reasons explain the blossoming of an area of research referred to as neuroeconomics (Glimcher et al. 2008).

In a nutshell, research in neuroeconomics aspires to describe the neurobiological processes and cognitive mechanisms that underlie economic choices. Although the field is still in its infancy, significant progress has been made already. Examples of economic choice include the choice between different ice cream flavors in a gelateria, the choice between different houses for sale, and the choice between different financial investments in a retirement plan. Notably, options available for choice in different situations can vary on a multitude of dimensions. For example, different flavors of ice cream evoke different sensory sensations and may be consumed immediately; different houses may vary for their price, their size, the school district, and the distance from work; different financial investment may carry different degrees of risk, with returns available in a distant, or not-so-distant, future. How does the brain generate choices in the face of this enormous variability? Economic and psychological theories of choice behavior have a cornerstone in the concept of value. While choosing, individuals assign values to the available options; a decision is then made by comparing these values. Hence, while options can vary on multiple dimensions, value represents a common unit of measure with which to make a comparison. From this perspective, understanding the neural mechanisms of economic choice amounts to describing how values are computed and compared in the brain.

Much research in recent years thus focused on the neural representation of economic value. As detailed in this review, a wealth of results obtained with a variety of techniques—single-cell recordings in primate and rodents, functional imaging in humans, lesion studies in multiple

species, etc.—indicates that neural representations of value exist in several brain areas and that lesions in some of these areas—most notably the orbitofrontal cortex (OFC) and ventromedial prefrontal cortex (vmPFC)—specifically impair choice behavior. In essence, the brain actually computes values when subjects make economic choices.

To appreciate the significance of this proposition, it is helpful to step back and consider a historical and theoretical perspective. Neoclassic economic theory can be thought of as a rigorous mathematical construct founded on a limited set of axioms (Kreps 1990). In this framework, the concept of value is roughly as follows. Under few and reasonable assumptions, any large set of choices can be accounted for as if the choosing subject maximized an internal value function. Thus values are central to the economist's description of choice behavior. Note, however, that the concept of value in economics is behavioral and analytical, not psychological. The fact that choices are effectively described in terms of values does not imply that subjects actually assign values while choosing. Thus by taking an “as if” stance, economic theory explicitly avoids stating what mental processes actually underlie choice behavior. The distinction between an “as if” theory and a psychological theory may seem subtle if not evanescent. However, this distinction is critical in economics, and it helps us to appreciate the contribution of recent research in neuroscience. The “as if” stance captures a fundamental limit: On the basis of behavior alone, values cannot be measured independently of choice. Consequently, the assertion that choices maximize values is intrinsically circular. The observation that values are actually computed in the brain essentially breaks this circularity. Indeed, once the correspondence between a neural signal and a behavioral measure of value has been established, that neural signal provides an independent measure of value, in principle dissociable from choices. In other words, the assertion that choices maximize values becomes potentially falsifiable and thus truly scientific (Popper 1963). For this reason, I view the discovery that

values are indeed encoded at the neural level as a major conceptual advance and perhaps the most important result of neuroeconomics to date.

With this perspective, the purposes of this article are threefold. First, I review the main experimental results on the neural mechanisms of value encoding and economic choice. Second, I place the current knowledge in a unifying framework, proposing a model of how economic choice may function at the neural level. And third, I indicate areas of current debate and suggest directions for future research. The article is organized as follows. The next section introduces basic concepts and outlines a good-based model of economic choice. The third section describes the standard neuroeconomic method used to assess the neural encoding of subjective value. The fourth section summarizes a large body of work from animal neurophysiology, human imaging, and lesion studies, which provides evidence for an abstract representation of value. The fifth section discusses the neural encoding of action values and their possible relevance to economic choice. The final section highlights open issues that require further experimental work. Overall, I hope to provide a comprehensive, though necessarily not exhaustive, overview of this field.

## ECONOMIC CHOICE: A GOOD-BASED MODEL

What cognitive and neural computations take place when individuals make economic choices? In broad strokes, my proposal is as follows. I embrace the view that economic choice is a distinct mental function (Padoa-Schioppa 2007) and that it entails assigning values to the available options. The central proposition of the model is that the brain maintains an abstract representation of “goods” and that the choice process—the computation and comparison of values—takes place within this space of goods. Thus I refer to this proposal as a good-based model of economic choice. I define a commodity as a unitary amount of a specified good independent of the circumstances in which it is available (e.g., quantity, cost, delay). The value

**OFC:** orbitofrontal cortex

**vmPFC:** ventromedial prefrontal cortex

**Good:** a commodity and a collection of determinants

**Good-based models:** values are computed and compared independent of the sensorimotor contingencies of choice (goods space). The choice outcome subsequently guides an action plan

**Action value:** a neuron encodes an action value if it is preferentially active when a particular action is planned and if it is modulated by the value associated with that action



**Determinant:**

a dimension on which goods may vary. During economic choice, different determinants are integrated into a subjective value

**Sensorimotor contingencies of choice:**

spatial location of the offers and motor description of the actions necessary to obtain the chosen good

**Action:** movement of the body in space, described by the kinematics and dynamics

**Menu invariance:**

holds true if values are assigned to different goods independently of one another. Menu invariance implies preference transitivity

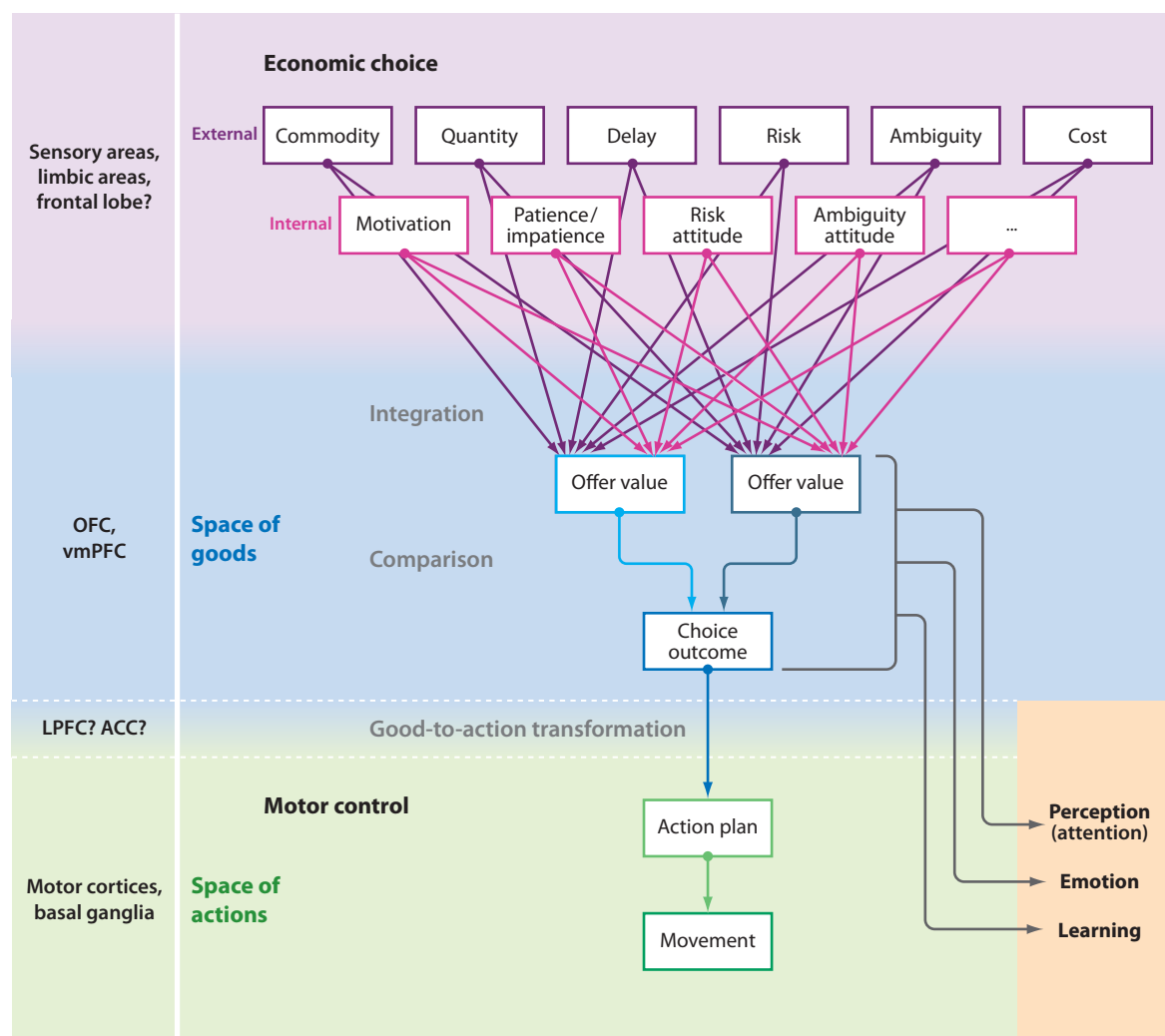
of each good is computed at the time of choice on the basis of multiple determinants, which include the specific commodity, its quantity, the current motivational state, the cost, the behavioral context of choice, etc. The collection of these determinants thus defines the good. While choosing, individuals compute the values of different options independently of one another. This computation does not depend on the sensorimotor contingencies of choice (the spatial configuration of the offers or the specific action that will implement the choice outcome). These contingencies may, however, affect values in the form of action costs (the actions necessary to obtain different goods often bear different costs). The model proposed here assumes that the action cost (i.e., the physical effort) is computed, represented in a nonspatial way, and integrated with other determinants in the computation of subjective value. According to the good-based model, computation and comparison of values take place within prefrontal regions, including the OFC, the vmPFC, and possibly other areas. The choice outcome—the chosen good and/or the chosen value—then guides the selection of a suitable action (good-to-action transformation). The good-based model, depicted in **Figure 1**, is thus defined by the following propositions:

1. Economic choice is a distinct mental function, qualitatively different from other overt behaviors that can be construed as involving a choice (e.g., perceptual decisions, associative learning). Economic choice entails assigning values to the available options.
2. A good is defined by a commodity and a collection of determinants that characterize the conditions under which the commodity is offered. Determinants can be either external (e.g., cost, time delay, risk, ambiguity) or internal to the subject (e.g., motivational state, (im)patience, risk attitude, ambiguity attitude).
3. The brain maintains an abstract representation of goods. More specifically, when a subject makes a choice, different sets of neurons represent the identities and

values of different goods. The ensemble of these sets of neurons provides a space of goods. This representation is abstract in the sense that the encoding of values does not depend on the sensorimotor contingencies of choice. Choices take place within this representation; values are computed and compared in the space of goods.

4. Some determinants may be learned through experience (e.g., the cost of a particular good), whereas other determinants may not be learned (e.g., the motivational state, the behavioral context). The process of value assignment implies an integration of different determinants. Thus the value of each good is computed “online” at the time of choice.
5. While choosing, individuals normally compute the values of different goods independently of one another. Such menu invariance implies transitive preferences.
6. Values computed in different behavioral conditions can vary by orders of magnitude. The encoding of value adapts to the range of values available in any given condition and thus maintains high sensitivity.
7. With respect to brain structures, the computation and comparison of values take place within prefrontal regions, including OFC, vmPFC, and possibly other regions. The choice outcome then guides a good-to-action transformation that originates in prefrontal regions and culminates in premotor regions, including parietal, precentral, and subcortical regions.
8. In addition to providing the bases for economic choices, subjective values inform a variety of neural systems, including sensory and motor systems (through attention and attention-like mechanisms), learning (e.g., through mechanisms of reinforcement learning), emotion (including autonomic functions), etc.

As illustrated below, this good-based model accounts for a large body of experimental results. It also makes several predictions that need to be tested in future work. In this respect, the



**Figure 1**

Good-based model. The value of each good is computed integrating multiple determinants, of which some are external (e.g., commodity, quantity, etc.) and others are internal (motivation, (im)patience, etc.). Offer values of different goods are computed independently of one another and then compared to make a decision. This comparison takes place within the space of goods. The choice outcome (chosen good, chosen value) then guides an action plan through a good-to-action transformation. Values and choice outcomes also inform other brain systems, including sensory and motor systems (through attention and attention-like mechanisms), associative learning (e.g., through mechanisms of reinforcement learning), emotion (including autonomic functions), etc. Abbreviations: orbitofrontal cortex (OFC), ventromedial prefrontal cortex (vmPFC), lateral prefrontal cortex (LPFC), anterior cingulate cortex (ACC).

good-based model proposed here should be regarded as a working hypothesis. Notably, my proposal differs from other models of economic choice previously discussed by other authors. Below, I highlight these differences and suggest possible approaches to assess the merits of different proposals.

### MEASURING ECONOMIC VALUE AND ITS NEURAL REPRESENTATION

Consider a person choosing between two houses for sale at the same price: One house is smaller but closer to work, and the other is

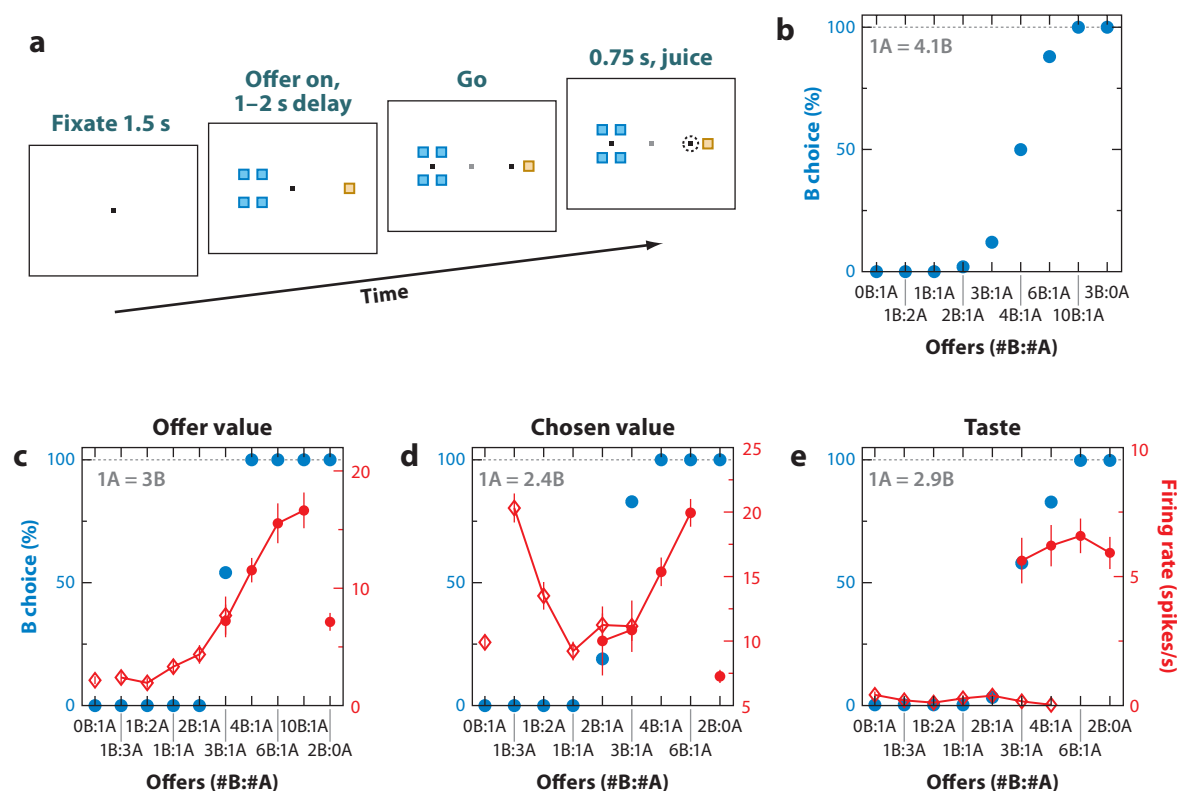
larger but further from work. All things being equal, the person would certainly prefer to live in a large house and close to work, but that option is beyond her budget. Thus while comparing houses to make a choice, the person must weigh against each other two dimensions, the distance from work and the square footage of the house. Physically, these two dimensions are different and incommensurable. However, the value that the chooser assigns to the two options provides a common scale, a way to compare the two dimensions. Thus intrinsic to the concept of value is the notion of a trade-off between physically distinct and competing dimensions (i.e., different determinants). This example also highlights two fundamental attributes of value. First, value is subjective. For example, one person may be willing to live in a smaller house to avoid a long commute, whereas another person may accept a long commute to enjoy a larger house. Second, measuring the subjective value assigned by a particular individual to a given good necessarily requires asking the subject to choose between that good and other options.

In recent years, neuroscience scholars have embraced these concepts and used them to study the neural encoding of economic value. In the first study to do so (Padoa-Schioppa & Assad 2006), we examined trade-offs between commodity and quantity. In this experiment, monkeys chose between two juices offered in variable amounts. The two juices were labeled A and B, with A preferred. When offered one drop of juice A versus one drop of juice B (offer 1A:1B), the animals chose juice A. However, the animals were thirsty; they generally preferred larger amounts of juice to smaller amounts of juice. The amounts of the two juices offered against each other varied from trial to trial, which induced a commodity-quantity trade-off in the choice pattern. For example, in one session (**Figure 2a,b**), offer types included 0B:1A, 1B:2A, 1B:1A, 2B:1A, 3B:1A, 4B:1A, 6B:1A, 10B:1A, and 3B:0A. The monkey generally chose 1A when 1B, 2B, or 3A were available as an alternative; it was roughly indifferent between the two juices when offered 4B:1A; and it

chose B when 6B or 10B was available. Thus the monkey assigned to 1A a value roughly equal to the value it assigned to 4B. A sigmoid fit provided a more precise indifference point:  $1A = 4.1B$  (**Figure 2b**). This equation established a relationship between juices A and B. On this basis, we computed a variety of value-related variables, which were then used to interpret the activity of neurons in the OFC. In particular, the analysis showed that neurons in this area encode three variables: offer value (the value of only one of the two juices), chosen value (the value chosen by the monkey in any given trial), and taste (a binary variable identifying the chosen juice) (**Figure 2c–e**).

In our experiment (**Figure 2**), offers varied on two dimensions: juice type (commodity) and juice amount (quantity). However, the same method can be applied when offers vary on other dimensions, such as probability, cost, delay, etc. For example, Kable & Glimcher (2007) conducted on human subjects an experiment on temporal discounting. People and animals often prefer smaller rewards delivered earlier to larger rewards delivered later, an important phenomenon with broad societal implications. In this study, subjects chose in each trial between a small amount of money delivered immediately and a larger amount of money delivered at a later time. For given delivery time  $T$ , the authors varied the amount of money and identified the indifference point (the amount of money delivered at time  $T$  such that the subject would be indifferent between the two options). The authors repeated this procedure for different delivery times  $T$ . Indifference points—fitted with a hyperbolic function—provided a measure of the subjective value choosers assigned to time-discounted money. During the experiment, the authors recorded the blood-oxygen-level-dependent (BOLD) signal. In the analyses, they used the measure of subjective value obtained from the indifference point as a regressor for the neural activity. Their results showed that the vmPFC encodes time-discounted values (see also Kim et al. 2008, Kobayashi & Schultz 2008, Louie & Glimcher 2010).





**Figure 2**

Measuring subjective values: value encoding in the orbitofrontal cortex (OFC). (a) Economic choice task. In this experiment, monkeys chose between different juices offered in variable amounts. Different colors indicated different juice types, and the number of squares indicated different amounts. In the trial depicted here, the animal was offered 4 drops of peppermint tea (juice B) versus 1 drop of grape juice (juice A). The monkey indicated its choice with an eye movement. (b) Choice pattern. The x-axis represents different offer types ranked by the ratio #B:#A. The y-axis represents the percent of trials in which the animal chose juice B. The monkey was roughly indifferent between 1A and 4B. A sigmoid fit indicated, more precisely, that  $1A = 4.1B$ . The relative value (4.1 here) is a subjective measure in multiple senses. First, it depends on the two juices. Second, given two juices, it varies for different individuals. Third, for any individual and two given juices, it varies depending, for example, on the motivational state of the animal (thirst). Thus to examine the neural encoding of economic values, it is necessary to examine neural activity in relation to the subjective values measured concurrently. (c) OFC neuron encoding the offer value. Blue circles indicate the behavioral choice pattern (*relative value in the upper left*), and red symbols indicate the neuronal firing rate. Hollow red diamonds and filled red circles refer, respectively, to trials in which the animal chose juice A and juice B. A linear relationship exists between the activity of the cell and the quantity of juice B offered to the monkey. (d) OFC neuron encoding the chosen value. A linear relationship exists between the activity of the cell and the value chosen by the monkey in each trial. For this session,  $1A = 2.4B$ . The activity of the cell was low when the monkey chose 1A or 2B, higher when the monkey chose 2A or 4B, and highest when the monkey chose 1A or 6B. Neurons encoding the chosen value are thus identified on the basis of the relative value of the two juices. (e) OFC neuron encoding the taste. The activity of the cell is binary depending on the chosen juice but independent of its quantity (panels d–e, same conventions as in panel c). Adapted from Padoa-Schioppa & Assad (2006), *Nature* (Nature Publishing Group), and from Padoa-Schioppa (2009), *Journal of Neuroscience* (used with permission from the Society for Neuroscience).

An interesting procedure to measure indifference points is to perform a “second price auction.” For example, in a study by Plassmann et al. (2007), hungry human subjects were asked

to declare the highest price they would be willing to pay for a given food (i.e., their indifference point, also called “reservation price”). Normally, people would try to save money and

declare a price lower than their true reservation price. However, second price auctions discourage them from doing so by randomly generating a second price after the subjects have declared their own price. If the second price is lower than the declared price, subjects get to buy the food and pay the second price; if the second price is higher than the declared price, subjects do not get to buy the food at all. In these conditions, the optimal strategy for subjects is to declare their true reservation price. This procedure thus measures for each subject the indifference point between food and money. Using this measure, Plassmann et al. confirmed that the BOLD signal in the OFC encodes the value subjects assigned to different foods (see also De Martino et al. 2009).

In summary, to measure the neural representation of subjective value, it is necessary to let the subject choose between alternative offers, infer values from the indifference point, and use that measure to interpret neural signals. This experimental method—used widely in primate neurophysiology (Kim et al. 2008, Kimmel et al. 2010, Klein et al. 2008, Kobayashi & Schultz 2008, Louie & Glimcher 2010, O'Neill & Schultz 2010, Sloan et al. 2010, Watson & Platt 2008) and human imaging (Brooks et al. 2010, Christopoulos et al. 2009, De Martino et al. 2009, FitzGerald et al. 2009, Gregorios-Pippas et al. 2009, Hsu et al. 2009, Levy et al. 2010, Peters & Buchel 2009, Pine et al. 2009, Shenhav & Greene 2010)—is now standard in neuroeconomics.

### AN ABSTRACT REPRESENTATION OF ECONOMIC VALUE

In this section, I review the evidence from neural recordings and lesion studies indicating that the representation of value in OFC and vmPFC is abstract and causally linked to economic choices. I then describe how this representation of value is affected by the behavioral context choice, and I discuss the evidence suggesting that values are computed online.

### Evidence From Neural Recordings

A neuronal representation of value can be said to be abstract (i.e., in the space of goods) if two conditions are met. First, the encoding should be independent of the sensorimotor contingencies of choice. In particular, the activity representing the value of any given good should not depend on the action executed to obtain that good. Second, the encoding should be domain general. In other words, the activity should represent the value of the good affected by all the relevant determinants (commodity, quantity, risk, cost, etc.). Current evidence for such an abstract representation is most convincing for two brain areas: OFC and vmPFC. In this subsection and the next, I review the main experimental results from, respectively, neural recordings and lesion studies.

In our original study (Figure 2), we examined a large number of variables that OFC neurons might possibly encode, including offer value, chosen value, other value (the value of the unchosen good), total value, value difference (chosen value minus unchosen value), taste, etc. Several statistical procedures were used to identify a small set of variables that would best account for the neuronal population. The results can be summarized as follows. First, offer value, chosen value, and taste accounted for the activity of neurons in the OFC significantly better than any other variable examined in the study. Any additional variable explained less than 5% of responses. Second, the encoding of value in OFC was independent of the sensorimotor contingencies of the task. Indeed, less than 5% of OFC neurons were significantly modulated by the spatial configuration of the offers on the monitor or by the direction of the eye movement. Third, each neuronal response encoded only one variable, and the encoding was linear. Indeed, a linear regression of the firing rate onto the encoded variables generally provided a very good fit, and adding terms to the regression (quadratic terms or additional variables) usually failed to improve the fit significantly. Fourth, the timing of the encoding appeared to match the mental processes monkeys presumably



undertook during each trial. In particular, neurons encoding the offer value—the variable on which choices were presumably based—were the most prominent immediately after the offers were presented to the animal (Padoa-Schioppa & Assad 2006).

With respect to the first condition—independence from sensorimotor contingencies—the evidence for an abstract representation of values thus seems robust. Indeed, consistent results were obtained in several other single-cell studies in primates (Grattan & Glimcher 2010, Kennerley & Wallis 2009, Roesch & Olson 2005).

With respect to the second condition—domain generality—current evidence for an abstract representation of value is clearly supportive. Indeed, domain generality has been examined extensively using functional imaging in humans. For example, Peters & Büchel (2009) let subjects choose between different money offers that could vary on two dimensions: delivery time and probability. Using the method described above, they found that neural activity in the OFC and ventral striatum encoded subjective values as affected by either delay or risk. In another study, Levy et al. (2010) let subjects choose between money offers that varied either for risk or for ambiguity. Using the same method, they found that the BOLD signal in vmPFC and ventral striatum encoded subjective values under both conditions. [More recent evidence suggests that the ventral striatum is not involved in choice per se (Cai et al. 2011).] De Martino et al. (2009) compared the encoding of subjective value when individuals gain or lose money—an important distinction because behavioral measures of value are typically reference-dependent (Kahneman & Tversky 1979). They found that OFC activity encoded the subjective value under either gains or losses. Taken together, these results consistently support a domain general representation of subjective value in OFC and vmPFC. As a caveat, I note that because of the low spatial resolution, functional imaging data cannot rule out that different determinants

of value might be encoded by distinct, but anatomically nearby, neuronal populations.

Several determinants of choice have also been examined at the level of single neurons. For example, Roesch & Olson (2005) delivered to monkeys different quantities of juice with variable delays. They found that OFC neurons were modulated by both variables and that neurons that increased their firing rates for increasing juice quantities generally decreased their firing rate for increasing time delays. Although the study did not provide a measure of subjective value, the results do suggest an integrated representation of value. In related work, Morrison & Salzman (2009) delivered to monkeys positive or negative stimuli (juice drops or air puffs). Consistent with domain generality, neuronal responses in the OFC had opposite signs. In another study, Kennerley et al. (2009) found a sizable population of OFC neurons modulated by three variables: the juice quantity, the action cost, and the probability of receiving the juice at the end of the trial. Notably, the firing rate generally increased as a function of the juice quantity and of the probability and decreased as a function of the action cost (or the other way around). Thus the modulation across determinants was congruent. Although these experiments did not measure subjective value, the results clearly support the notion of a domain-general representation.

In conclusion, a wealth of empirical evidence is consistent with the notion that OFC and vmPFC harbor an abstract representation of value, although the issue of domain generality needs confirmation at the level of single cells and for determinants not yet tested. Interestingly, insofar as a representation of value exists in rodents (Schoenbaum et al. 2009, van Duuren et al. 2007), it does not appear to meet the conditions for abstraction defined here. Indeed, several groups found that neurons in the rodent OFC are spatially selective (Feierstein et al. 2006, Roesch et al. 2006). Furthermore, experiments that manipulated two determinants of value found that different neuronal populations in the rat OFC represent

reward magnitude and time delay—a striking difference with primates (Roesch et al. 2006, Roesch & Olson 2005). The reasons for this discrepancy are not clear (Zald 2006). However, Wise (2008) noted that the architecture of the orbital cortex in rodents and primates is qualitatively different, which suggests that an abstract representation of value emerged late in evolution in parallel with the expansion of the frontal lobe. At the same time, it cannot be excluded that domain-general value signals exist in other regions of the rodent brain.

### Evidence From Lesion Studies

While establishing a link between OFC and vmPFC and the encoding of value, the evidence reviewed so far does not demonstrate a causal relationship between neural activity in these areas and economic choices. Such relationship emerges from lesion studies. In this respect, one of the most successful experimental paradigms is that of reinforcer devaluation. In these experiments, animals choose between two different foods. During training sessions, animals reveal their normal preferences. Before test sessions, however, animals are given free access to their preferred food. Following such selective satiation, control animals switch their preferences and choose their usually-less-preferred food. In contrast, in animals with OFC lesions, this satiation effect disappears. After OFC lesions, animals continue to choose the same food and thus seem incapable of computing values. This result has been replicated by several groups in both rodents (Gallagher et al. 1999, Pickens et al. 2003) and monkeys (Izquierdo et al. 2004; Kazama & Bachevalier 2009; Machado & Bachevalier 2007a,b). Notably, OFC lesions specifically affect value-based decisions as distinguished, for example, from strategic (i.e., rule-based) decisions (Baxter et al. 2009) or from perceptual judgments (Fellows & Farah 2007).

In the scheme of **Figure 1**, selective satiation alters subjective values by manipulating the motivational state of the animal. However, OFC lesions disrupt choice behavior also when trade-offs involve other determinants of

value. For example, with respect to risk, several groups reported that patients with OFC lesions present atypical risk-seeking behavior (Damasio 1994, Rahman et al. 1999). Along similar lines, Hsu et al. (2005) found that OFC patients are much less adverse to ambiguity compared with normal subjects. OFC lesions affect choices also when the trade-off involves a social determinant such as fairness, as observed in the ultimatum game (Koenigs & Tranel 2007). With respect to time delays, OFC patients are sometimes described as impulsive (Berlin et al. 2004). However, animal studies on the effects of OFC lesions on intertemporal choices provide diverse results. Specifically, Winstanley et al. (2004) found that rats with OFC lesions are more patient than control animals, whereas Mobini et al. (2002) found the opposite effect. Notably, Winstanley et al. trained animals before the lesion, whereas Mobini et al. trained animals after the lesion. Moreover, in another study, Rudebeck et al. (2006) found that intertemporal preferences following OFC lesions are rather malleable; lesioned animals that initially seemed more impulsive than controls became indistinguishable from controls after performing in a forced-delay version of the task. In the scheme of **Figure 1**, these results may be explained as follows. Choices are normally based on values integrated in the OFC. Absent the OFC, animals choose in a not-value-based fashion, with one determinant taking over. Training affects what option animals default to when OFC is ablated.

One determinant of choice for which current evidence is arguably more controversial is action cost. Arguments against domain generality have been based in particular on two sets of experiments conducted by Rushworth and colleagues. In a first experiment (Rudebeck et al. 2006, Walton et al. 2002), rats could choose between two possible options, one of which was more effortful but more rewarding. The authors found that the propensity to choose the effortful option was reduced after lesions to the anterior cingulate cortex (ACC) but was not significantly altered after OFC lesions. In another study (Rudebeck et al. 2008), the authors tested

monkeys with ACC or OFC lesions in two variants of a matching task, in which the correct response was identified either by a particular object (object-based) or by a particular action (action-based). Both sets of lesions reduced performance in both tasks. However, ACC lesions had a comparatively higher effect on the action-based than on the object-based variant, whereas the contrary was true for OFC lesions. On this basis, several investigators proposed that stimulus values (i.e., good values defined disregarding action costs) and action costs are computed separately, in OFC and ACC respectively (Rangel & Hare 2010, Rushworth et al. 2009). Although this proposal deserves further examination, it can be noted that the results of Rushworth and colleagues do not actually rule out a domain-general representation of value in the OFC. Indeed, as illustrated above for intertemporal choices, ablating a valuation center does not necessarily lead to a consistent bias for or against one determinant of value. Thus the results of the first experiment (Rudebeck et al. 2006)—which, in fact, have not been replicated in primates (Kennerley et al. 2006)—do implicate the ACC in some computation related to action costs but are not conclusive on the OFC. Conversely, the second study (Rudebeck et al. 2008) is less obviously relevant to the issue of value encoding because matching tasks do not necessarily require an economic choice in the sense defined here. Indeed, in matching tasks, there is always a correct answer; subjects are required to infer it from previous trials, not to state a subjective preference (Padoa-Schioppa 2007). Even assuming that animals undertake in matching tasks the same cognitive and neural processes underlying economic choice, it is difficult to establish whether impairments observed after selective brain lesions are due to deficits in learning or in choosing. Finally, in the study of Rudebeck et al. (2008), the action-based variant of the task was much more difficult than the object-based variant of the task (many more errors), and OFC lesions disrupted performance in both variants. Hence, it is possible that OFC lesions selectively interfered with the choice component of the task (and thus

affected both variants equally), whereas ACC lesions affected only the action-based variant. In conclusion, current evidence on choices in the presence of action cost can certainly be reconciled with the hypothesis that OFC harbors an abstract and domain-general representation of subjective value.

To summarize, OFC and vmPFC lesions disrupt choices as defined by a variety of different determinants. Although lesion studies typically lack fine spatial resolution, the results are generally consistent with a domain-general representation of subjective value. Most important, the disruptive effect of OFC and vmPFC lesions on choice behavior establishes a causal link between the neuronal representation of subjective value found by neural recordings in these areas and economic choices.

### Choosing in Different Contexts: Menu Invariance and Range Adaptation

The results reviewed in the previous sections justify the hypothesis that choices are based on values computed in OFC and vmPFC. Notably, different neurons in the OFC encode different variables (**Figure 2**). In a computational sense, the valuation stage underlying the choice is captured by neurons encoding the offer value. Thus according to the current hypothesis, choices are based on the activity of these neurons. In this respect, a critical question is whether and how the encoding of value depends on the behavioral context of choice. There are at least two aspects to this issue.

First, for any given offer, a variety of different goods may be available as an alternative. For example, in a gelateria, a person might choose between nocciola and pistacchio or, alternatively, between nocciola and chocolate. A critical question is whether the value a subject assigns to a given good depends on what other good is available as an alternative (i.e., on the menu). Notably, this question is closely related to another critical question: whether preferences are transitive. Given three goods A, B, and C, transitivity holds true if  $A > B$  and  $B > C$  imply  $A > C$

**Preference**

**transitivity:** for any 3 goods X, Y, and Z,  $X > Y$  and  $Y > Z$  imply  $X > Z$  ( $>$  indicates “is preferred to”).

Transitivity is the hallmark of rational decision making

(where  $>$  stands for “is preferred to”). Preference transitivity is a hallmark of rational choice behavior and one of the most fundamental assumptions of economic theory (Kreps 1990). Transitivity and menu invariance are closely related because preferences may violate transitivity only if values depend on the menu (Grace 1993, Tversky & Simonson 1993). Although transitivity violations can sometimes be observed (Shafir 2002, Tversky 1969), in most circumstances human and animal choices indeed satisfy transitivity. In a second study, we showed that the representation of value in the OFC is invariant for changes of menu (Padoa-Schioppa & Assad 2008). In this experiment, monkey chose among 3 juices labeled A, B, and C, in decreasing order of preference. Juices were offered pairwise, and trials with the 3 juice pairs (A:B, B:C, and C:A) were interleaved. Neuronal responses encoding the offer value of one particular juice typically did not depend on the juice offered as an alternative (**Figure 3**), and similar results were obtained for chosen value neurons and taste neurons. If choices are indeed based on values encoded in the OFC, menu invariance may thus be the neurobiological origin of preference transitivity. Corroborating this hypothesis, Fellows & Farah (2007) found that patients with OFC lesions asked to express preference judgments for different foods violate transitivity significantly more often than do both control subjects and patients with dorsal prefrontal lesions—an effect not observed with perceptual judgments (e.g., in the assessment of different colors).

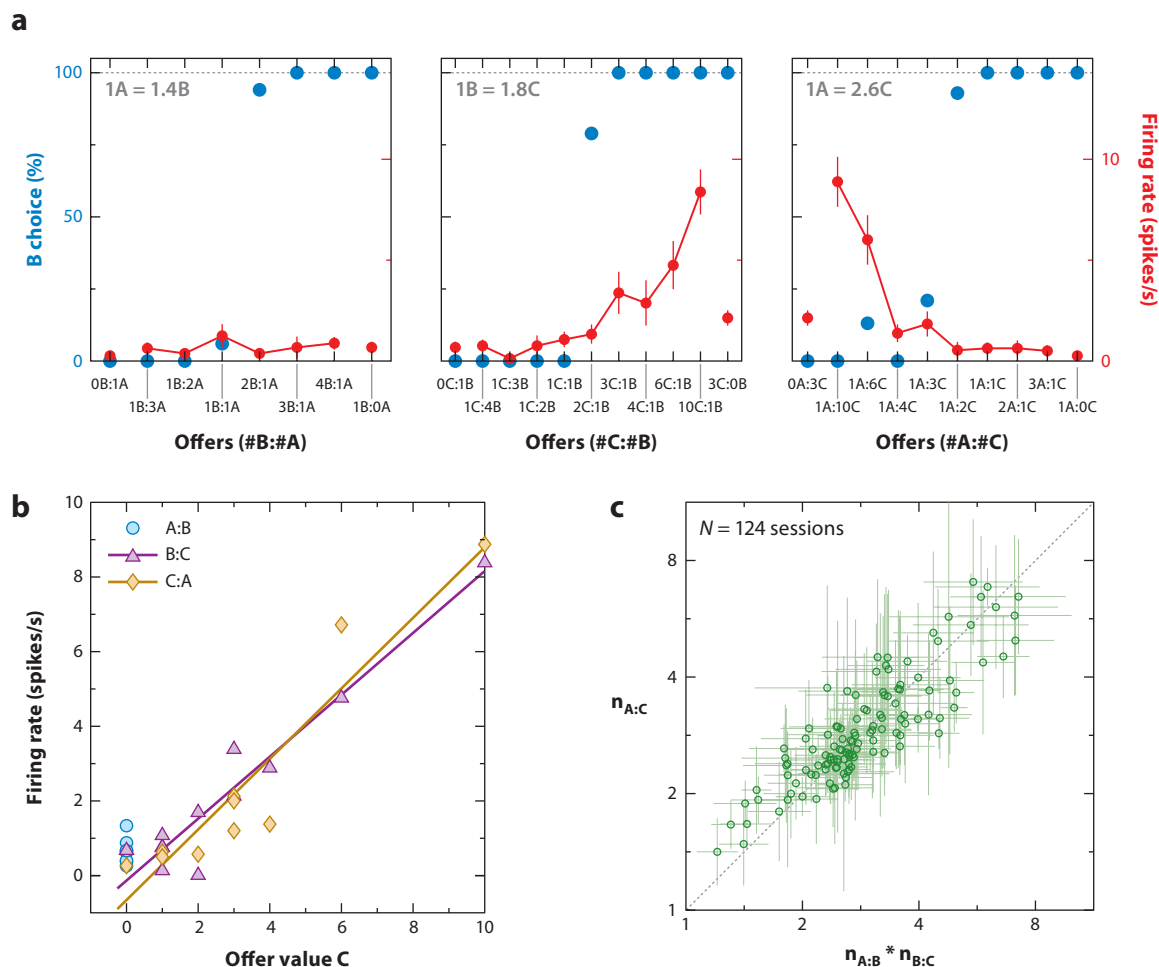
Second, values computed in different behavioral conditions can vary substantially. For example, the same individual may choose sometimes between goods worth a few dollars (e.g., when choosing between different ice cream flavors in a gelateria) and other times between goods worth many thousands of dollars (e.g., when choosing between different houses for sale). At the same time, any representation of value is ultimately limited to a finite range of neuronal firing rates. Moreover, given a range of possible values, an optimal (i.e., maximally sensitive) representation of value would fully

exploit the range of possible firing rates. These considerations suggest that the neuronal encoding of value may adapt to the range of values available in any given condition—a hypothesis I recently confirmed (Padoa-Schioppa 2009). The basic result is illustrated in **Figure 4**, which depicts the activity of 937 offer value neurons from the OFC. Different neurons were recorded in different sessions, and the range of values offered to the monkey varied from session to session. Yet, the distribution of activity ranges measured for the population did not depend on the range of values offered to the monkey. OFC neurons adapted their gain (i.e., the slope of the linear encoding) in such a way that a given range of firing rates described different ranges of values in different behavioral conditions. Corroborating results of Kobayashi et al. (2010) indicate that this adaptation can take place within 15 trials. Interestingly, neuronal firing rates in OFC do not depend on whether the encoded juice is preferred or nonpreferred in that particular session (Padoa-Schioppa 2009).

It has often been discussed whether the brain represents values as relative or absolute (Seymour & McClure 2008). This question can be rephrased by asking which parameters of the behavioral context do or do not affect the encoding of value. The results illustrated here indicate that the encoding of value in the OFC is menu invariant and range adapting. Importantly, although menu invariance and range adaptation hold in normal circumstances, when preferences are stable and transitive, these neural properties may be violated in the presence of choice fallacies (Camerer 2003, Frederick et al. 2002, Kahneman & Tversky 2000, Tversky & Shafir 2004)—a promising topic for future research (Kalenscher et al. 2010).

### Online Computation of Economic Values

Although they indicate that an abstract representation of good values is encoded in prefrontal areas, the results discussed so far do not address how this representation is formed. In this respect, two broad hypotheses can be



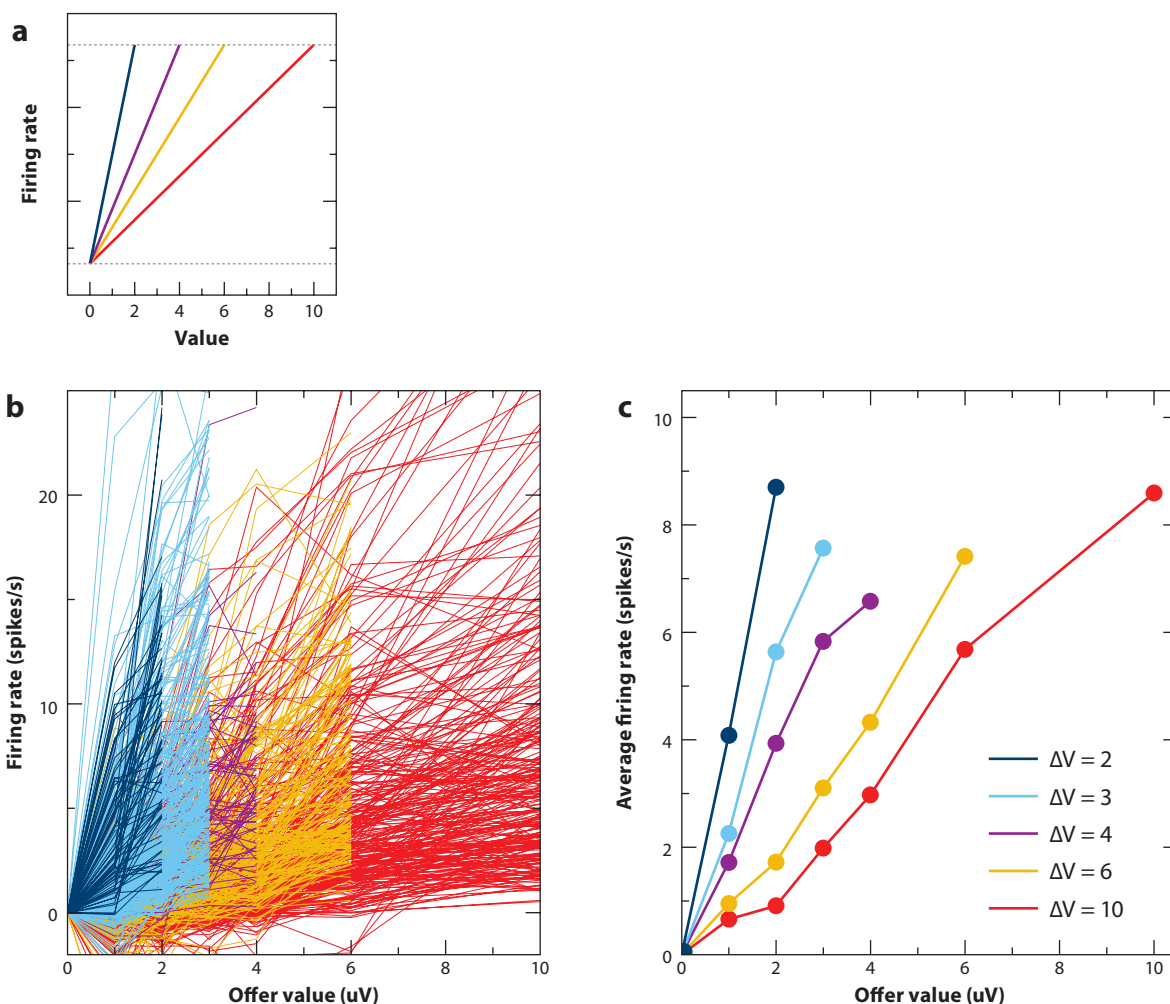
**Figure 3**

Menu invariance and preference transitivity. (a) One neuron encoding the offer value. In this experiment, monkeys chose between 3 juices (A, B, and C) offered pairwise. The three panels refer, respectively, to trials A:B, B:C, and C:A. In each panel, the x-axis represents different offer types, blue circles indicate the behavioral choice pattern, and red symbols indicate the neuronal firing rate. This neuron encodes the variable offer value C independently of whether juice C is offered against juice B or juice A. In trials A:B, the cell activity is low and not modulated. (b) Linear encoding. Same neuron as in panel a, with the firing rate (y-axis) plotted against the encoded variable (x-axis) separately for different juice pairs (indicated by different symbols, see legend). (c) Value transitivity. For each juice pair X:Y, the relative value  $n_{XY}$  is measured from the indifference point. The three relative values satisfy transitivity if (in a statistical sense)  $n_{AB} * n_{BC} = n_{AC}$ . In this scatter plot, each circle indicates one session ( $\pm$  SD) and the two axes indicate, respectively,  $n_{AB} * n_{BC}$  and  $n_{AC}$ . Data lie along the identity line, indicating that subjective values measured in this experiment satisfy transitivity. Choices based on a representation of value that is menu invariant are necessarily transitive. Adapted from Padoa-Schioppa & Assad (2008), *Nature Neuroscience* (Nature Publishing Group).

entertained. One possibility is that values are learned through experience and retrieved from memory at the time of choice. Alternatively, values could be computed online at the time of choice. In observance with a long tradition

in experimental psychology (Skinner 1953, Sutton & Barto 1998), referred to as behaviorism, economic choice is often discussed within the framework of, or as intertwined with, associative learning (Glimcher 2008, Montague





**Figure 4**

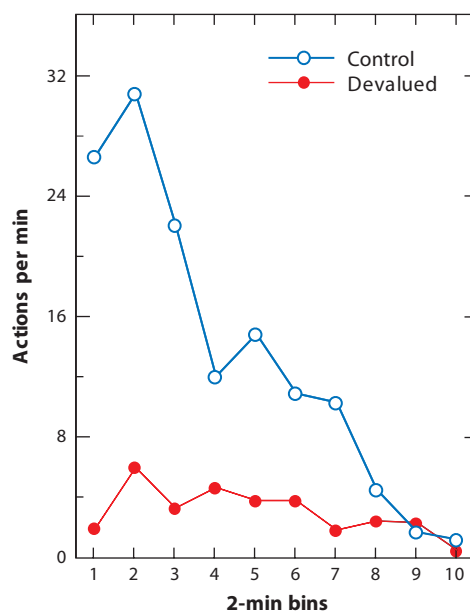
Range adaptation in the valuation system. (a) Model of neuronal adaptation. The cartoon depicts the activity of a value-encoding neuron adapting to the range of values available in different conditions. The x-axis represents value, the y-axis represents the firing rate, and different colors refer to different value ranges. In different conditions, the same range of firing rates encodes different value ranges. (b) Neuronal adaptation in the orbitofrontal cortex. The figure illustrates the activity of 937 offer value responses. Each line represents the activity of one neuron (y-axis) plotted against the offer value (x-axis). Different responses were recorded with different value ranges (see color labels). Although activity ranges vary widely across the population, the distribution of activity ranges does not depend on the value range. (c) Population averages. Each line represents the average obtained from neuronal responses in panel b. Adaptation can be observed for any value because average responses are separated throughout the value spectrum. Similar results were obtained for neurons encoding the chosen value. Adaptation was also observed for individual cells recorded with different value ranges (not shown). Adapted from Padoa-Schioppa (2009), *Journal of Neuroscience* (used with permission from the Society for Neuroscience).

et al. 2006, Rangel et al. 2008). Indeed, it is often assumed that subjective values are learned and retrieved from memory. Several considerations suggest, however, that values are more likely not learned and retrieved, but rather computed

online at the time of choice. Intuitively, this proposition follows from the fact that people and animals choose often and effectively between novel goods and/or in novel situations. Consider, for example, a person choosing

between two possible cocktails in a bar. The person might be familiar with both drinks. Yet, her choice will likely depend on unlearned determinants such as the motivational state (e.g., does she “feel like” a dry or sweet drink at this time), the behavioral context (e.g., what cocktail did her friend order), etc. Thus describing her choice on the basis of learned-and-retrieved values seems difficult.

Experimental evidence for values being computed online comes from an elegant series of studies conducted by Dickinson, Rescorla, Balleine, and their colleagues on reinforcer devaluation in rats (Adams & Dickinson 1981, Balleine & Ostlund 2007, Colwill & Rescorla 1986). In the simplest version of the experiment, animals were trained to perform a task (e.g., pressing a lever) to receive a given food. Subsequently, the animals were selectively satiated with that food and tested in the task. Critically, animals were tested “in extinction” (the food was not actually delivered upon successful execution of the task). Thus the performance of the animals gradually degraded over trials during the test phase. Most important, however, the performance of satiated animals was significantly lower than that of control animals throughout the test phase (Figure 5). In other words, satiated animals assigned to the food a lower value compared with that assigned by controls—an interpretation confirmed by a variety of control studies and in a free-choice version of the experiment (Balleine & Dickinson 1998). To my understanding, this result is at odds with the hypothesis that values are learned during training, stored in memory, and simply retrieved at the time of choice. Indeed, if this were the case, rats would retrieve in the test phase the value learned in the training phase, which is the same for experimental animals and control animals. In contrast, this result suggests that animals compute values online on the basis of both current motivation and previously acquired knowledge (see sidebar, Further Discussion on Reinforcer Devaluation). Adams (1982) also found that overtraining, which presumably turned choice into a habit, made animals insensitive to devaluation.



**Figure 5**

Effects of selective devaluation. In the training phase of this study, rats learned to perform a task (lever press or chain pull) to obtain a reward (food pellet or starch, in a counterbalanced design). Before testing, animals were selectively satiated with one of the two foods (devaluation). They were then tested in extinction. Thus their performance, measured in actions per minute (y-axis), dropped over time (x-axis) for either food reward. Critically, the performance for the devalued food (red filled symbols) was consistently below that for the control food (blue empty symbols). Adapted from Balleine & Dickinson (1998), *Neuropharmacology* (used with permission from Elsevier).

In summary, intuition and empirical evidence suggest that subjective values are computed online at the time of choice, not learned and retrieved from memory. However, more work is necessary to understand how the neural systems of valuation and associative learning interact and inform each other. Most important for the present purposes, the neural mechanisms by which different determinants—including learned and unlearned determinants—are integrated in the computation of values remain unknown. Although these mechanisms likely involve a variety of sensory, limbic, and association

## FURTHER DISCUSSION ON REINFORCER DEVALUATION

If values were learned and retrieved from memory, the results obtained in studies of reinforcer devaluation (**Figure 5**) would have to be interpreted with the assumption that during the devaluation phase the brain automatically updates stored values to reflect the new motivational state. However, this hypothesis seems hardly credible if one considers the fact that the motivational appeal of different goods is in perpetual evolution. For example, the value an individual would assign to any given food changes many times a day, during and after every meal, every time the individual exercises, or simply over time as sugar levels in the bloodstream get lower. Thus the hypothesis that values are learned and retrieved implies that the brain holds and constantly updates a large look-up table of values—a rather expensive design. The hypothesis put forth here—that values are computed only when needed—appears more parsimonious.

areas, further research is necessary to shed light on this critical aspect of choice behavior.

## ACTION VALUES AND THEIR POSSIBLE RELEVANCE TO ECONOMIC CHOICE

As reviewed in the previous section, a defining trait of the representation of value found in the OFC and the vmPFC is that values are encoded independently of the sensorimotor contingencies of choice. In contrast, in other brain areas, values modulate neuronal activity that is primarily sensory and/or motor. Such “nonabstract” representations have been found in numerous regions, including the dorsolateral prefrontal cortex (Kim et al. 2008, Leon & Shadlen 1999), the anterior cingulate cortex (Matsumoto et al. 2003, Seo & Lee 2007, Shidara & Richmond 2002), the posterior cingulate cortex (McCoy et al. 2003), the lateral intraparietal area (Louie & Glimcher 2010, Sugrue et al. 2004), the dorsal premotor area, the supplementary motor area, the frontal eye fields (Roesch & Olson 2003), the supplementary eye fields (Amador et al. 2000), the superior colliculus (Ikeda &

Hikosaka 2003, Thevarajah et al. 2010), the striatum (Kawagoe et al. 1998, Kim et al. 2009, Lau & Glimcher 2008, Samejima et al. 2005), and the centromedian nucleus of the thalamus (Minamimoto et al. 2005). A comprehensive review of all the relevant work is beyond my current purpose. However, I discuss here the possible significance of these value representations for economic choice.

Nonabstract value modulations are often interpreted in the “space of actions.” In other words, the spatially selective component of the neural activity is interpreted as encoding a potential action, and the value modulation is interpreted as a bias contributing to the process of action selection. Thus many experimental results have been or can be described in terms of action values. In broad terms, a neuron can be said to encode an action value if it is preferentially active when a particular action is planned and if it is modulated by the value associated with that action. Influential theoretical accounts posit that decisions are made ultimately on the basis of action values (Kable & Glimcher 2009, Rangel & Hare 2010). According to these action-based models, values are attached to different possible actions in the form of action values, and the decision—the comparison between values—unfolds as a process of action selection. This view of economic choice is clearly in contrast with the good-based proposal. Thus it is important to discuss whether current evidence for the neuronal encoding of action values can be reconciled with the good-based model proposed here. In this respect, a few considerations are needed.

First, in some cases, spatially selective signals modulated by value may be better interpreted as sensory rather than motor. In perceptual domains, value modulates activity by the way of attention—a more valuable visual stimulus inevitably draws higher attention. Thus such value signals may be best described in terms of spatial attention (Maunsell 2004). For example, neurons in the lateral intraparietal area (LIP) activate both in response to visual stimuli placed in their response field and in anticipation of an eye movement. Value modulations

recorded in economic choice tasks are strong during presentation of the visual stimulus and significantly lower before the saccade, when movement-related activity dominates (Louie & Glimcher 2010). This observation suggests that value modulates activity in this area by way of attention, a view bolstered by the fact that value modulations in LIP are normalized as predicted by psychophysical theories of attention (Bundesen 1990, Dorris & Glimcher 2004). Similar arguments may apply to other brain areas where neural activity interpreted in terms of action values is most likely not genuinely motor.

Second, action values possibly relevant to economic choice should be distinguished from action values defined in the context of reinforcement learning (RL) (Sutton & Barto 1998). Models of RL typically describe an agent facing a problem with multiple possible actions, one of which is objectively correct. In this context, an action value is an estimate of future rewards for a given action, and the agent learns action values by trial and error. According to behaviorism, any behavior, including economic choice, results from stimulus-response associations. Thus the behaviorist equates action values defined in RL to action values possibly relevant to economic choice. As noted above, a general problem with the behaviorist account is that people and animals can and often do choose effectively between novel goods. The RL variant of this account has the additional problem that choosing a particular good may require different actions at different times. For these reasons, action values possibly relevant to economic choice cannot be equated to action values defined in RL. Consequently, evidence for neuronal encoding of action values gathered using tasks that include a major learning component—instrumental conditioning (Samejima et al. 2005), dynamic matching tasks (Lau & Glimcher 2008, Sugrue et al. 2004), or n-armed bandit tasks—and obtained inferring values from RL models must be considered with caution. This issue is particularly relevant for brain regions, such as the dorsal striatum, that have been clearly linked to associative learning as distinguished from

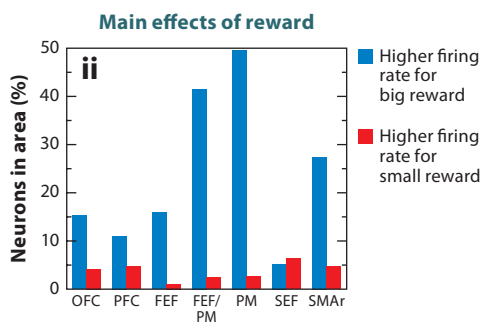
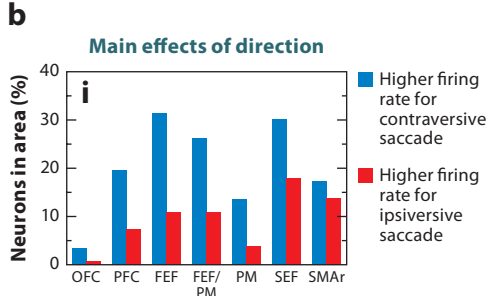
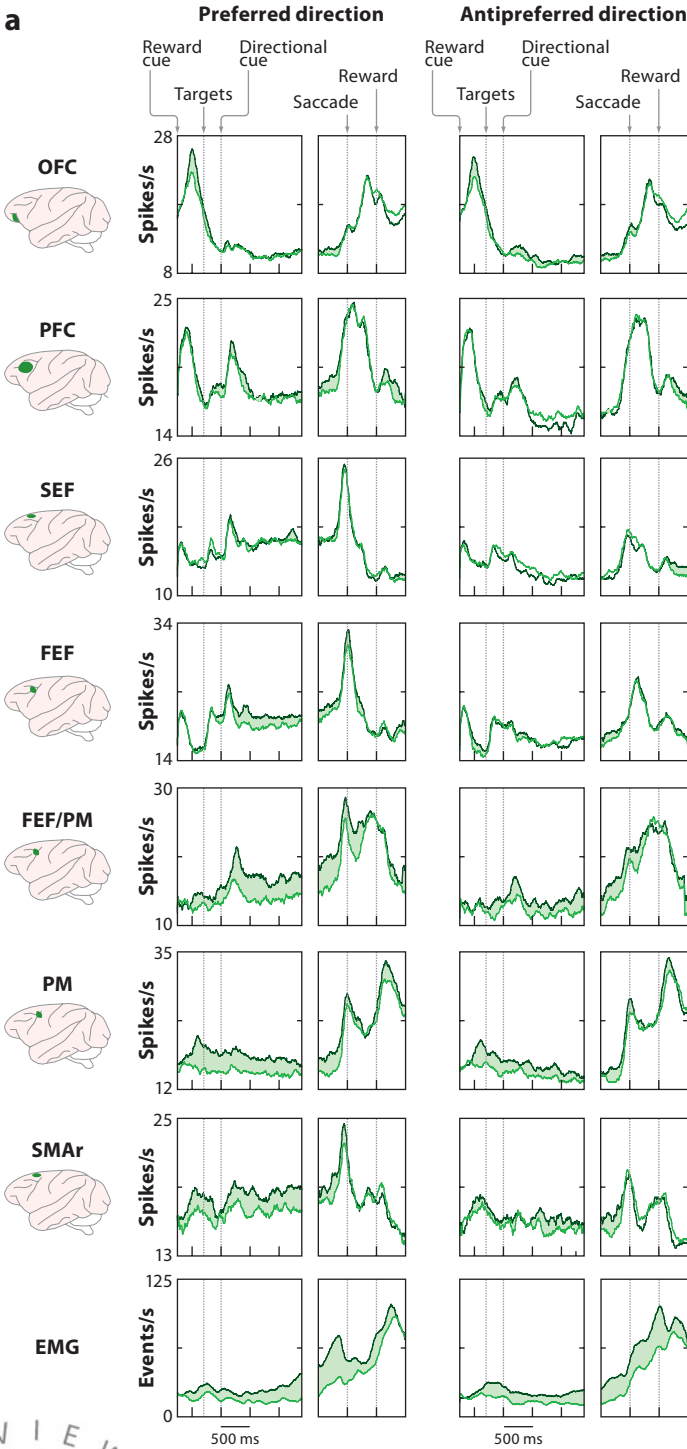
action selection (Kim et al. 2009, Williams & Eskandar 2006).

Third and most important, value signals can modulate physiological processes downstream of and unrelated to the decision. A compelling example is provided by Roesch & Olson (2003), who trained three monkeys in a variant of the memory saccade task. At the beginning of each trial, a cue indicated whether the amount of juice delivered for a correct response would be large or small. The authors found neuronal modulations consistent with action values in the frontal eye fields, the supplementary eye fields, the premotor cortex, and the supplementary motor area. Strikingly, modulations consistent with action values were also found in the electromyographic (EMG) activity of neck and jaw muscles (**Figure 6**), which suggests that value modulations recorded in cortical motor areas in this experiment—and possibly in other experiments—may be downstream of and unrelated to any decision in the sense defined here.

Taken together, these considerations suggest that evidence for the neural encoding of action values and their possible relevance to economic choices should be vetted against alternative hypotheses. With this premise, what evidence is necessary to hypothesize that an action value signal contributes to economic choice in the sense postulated by action-based models? It is reasonable to require three minimal conditions: (*a*) Neural activity must be genuinely motor, (*b*) neural activity must be modulated by subjective value, and (*c*) neural activity must not be downstream of the decision. These three conditions provide a more restrictive definition of action value. To my knowledge, evidence of neuronal activity satisfying these three conditions has never been reported. In fact, even relaxing condition *b*, I am not aware of any result that satisfies both conditions *a* and *c*. In particular, for activity encoding action values recorded in genuinely motor regions (which presumably satisfied condition *a*), it is generally difficult to rule out that responses were computationally downstream of the decision process (see sidebar, Separation Between Decision

**Action-based models:** economic decisions are made by comparing action values





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Making and Action Planning in Other Mental Functions).

In summary, neural activity encoding action values can contribute to a decision if it encodes action, it encodes value, and it does not follow the decision. Of course, the current lack of evidence for such neural activity, per se, does not falsify action-based models of economic choice. At the same time, current evidence on the encoding of action values can certainly be reconciled with the good-based model and thus does not challenge the present proposal.

## OPEN QUESTIONS AND DEVELOPMENTS

As illustrated in the previous sections, the good-based model explains a wealth of experimental results in the literature. At the same time, many aspects of this model remain to be tested. In this section, I briefly discuss two issues that seem particularly urgent.

Perhaps the most distinctive trait of the good-based model is the proposal that values are compared in the space of goods, independent of the actions necessary to implement choices. In this view, action values do not contribute to economic choice per se. Thus the good-based model is in contrast with action-based models, according to which choices are ultimately made by comparing the value of different action plans (Glimcher et al. 2005,

Rangel & Hare 2010). Ultimately, assessing between the two models requires tasks that can (in principle) dissociate in time economic choice from action planning. Consistent with the current proposal, recent work suggests that choices can be made independent of action planning (Cai & Padoa-Schioppa 2010, Wunderlich et al. 2010). Many aspects of this issue, however, remain to be clarified. For example, in many situations, goods available for choice require courses of action associated with different costs. The hypothesis put forth here—that action costs are integrated with other determinants of value in a nonspatial representation—remains to be tested. Also, in most circumstances, a choice ultimately leads to an action. Thus if choices indeed take place in the space of goods, a fundamental question is how choice outcomes are transformed into action plans. The good-to-action transformation, or series of transformations, is poorly understood and should be investigated in future work.

Another important issue is the relative role of OFC and vmPFC in economic choice and value-guided behavior. These two regions roughly correspond to two anatomically defined networks named, respectively, the orbital network (OFC) and the medial network (vmPFC) (Ongur & Price 2000). In an elegant series of studies, Price and colleagues showed that these two networks have distinct and largely segregated anatomical connections

### Action plan:

specification of an intended movement. Its neural representation reflects the spatial nature of the action

Figure 6

Action value signals downstream of the decision. (a) Activity profiles from the orbitofrontal cortex (OFC), the lateral prefrontal cortex (PFC), the supplementary eye fields (SEF), the frontal eye fields (FEF), the premotor cortex (PM), the supplementary motor area (SMA), and the muscle's electromyographic activity (EMG). For each brain region, dark green and light green refer, respectively, to trials with high and low value. Left and right panels refer to saccades toward, respectively, the preferred and antipreferred directions. For each area, the overall difference between the activity observed in the left and right panels (highlighted in *bi*) can be interpreted as encoding the action. The difference between the dark green and light green traces (light green area, highlighted in *bii*) is a value modulation. (b) Summary of action value signals. The top panel (*bi*) highlights the encoding of possible actions (*contraversive and ipsiversive for blue and red bars, respectively*). The bottom panel (*bii*) highlights value modulations (*positive and negative encoding for blue and red bars, respectively*). Action encoding is minimal in the OFC but significant in all motor areas. In contrast, value modulation is significant both in the OFC and in motor areas. Notably, there is a strong value modulation also in the EMG (bottom panels in panel *a*). Muscles certainly do not contribute to economic choice—a clear example of action value unrelated to the decision. Thus value modulations in the motor areas—which ultimately control the motor output—are most likely related to value modulations in the EMG not to the decision process per se. Adapted from Roesch & Olson (2003, 2005), *Journal of Neurophysiology* (used with permission from the American Physiology Society).

## SEPARATION BETWEEN DECISION MAKING AND ACTION PLANNING IN OTHER MENTAL FUNCTIONS

The observation that decision making is separable from action planning appears to remain valid beyond the domain of economic choice. Indeed, neural activity recorded during different tasks that involve a decision generally violates condition *a* (the activity should be genuinely motor) and/or condition *c* (the activity should not be downstream of the decision). Consider, for example, condition *c*. To demonstrate that a neural process satisfies it, it is necessary to design experiments that can—at least in principle—dissociate in time between decision making and action planning (Bennur & Gold 2011, Cai & Padoa-Schioppa 2010, Cisek & Kalaska 2002, Gold & Shadlen 2003, Horwitz et al. 2004, Wunderlich et al. 2010). Evidence that decisions cannot be made in the absence of action planning would support the action-based hypothesis (i.e., that decision making is embedded in motor or premotor systems). However, we are not aware of any such evidence. In fact, several studies found evidence to the contrary. For example, recent results by Bennur & Gold (2011) demonstrate that perceptual decisions can occur in the absence of any action planning. In another study, Cisek & Kalaska (2002) explicitly designed a task to satisfy condition *c* and obtained results that strikingly violate condition *a*. In their experiment, monkeys were first shown two potential targets for a reaching movement. Subsequently, the ambiguity was resolved in favor of one of the two targets. Insofar as this task requires a “decision,” neurons encoding potential movements prior to the final instruction would be consistent with the decision unfolding as a process of action selection. Remarkably, the authors did not find any evidence for such neurons. Indeed, cells in motor and premotor cortices (areas F1 and F2) did not activate before the final instruction. Conversely, neurons that activated prior to the final instruction were from prefrontal cortex (area F7) and thus most likely not motor (Picard & Strick 2001).

(Price & Drevets 2010). The orbital network receives inputs from nearly all sensory modalities and from limbic regions, consistent with a role in integrating different determinants into a value signal. In contrast, the medial network is strongly interconnected with the hypothalamus and brain stem, suggesting a role in the control of autonomic functions and visceromotor responses (Price 1999). Indeed, neural activity

in this region is known to correlate with heart rate and skin conductance (Critchley 2005, Fredrikson et al. 1998, Ziegler et al. 2009). The relationship between decision making, emotion, and autonomic functions, while often discussed, remains substantially unclear. One possibility is that autonomic responses play a direct role in decision making (Damasio 1994). Another possibility is that values and decisions, made independently, inform emotion and autonomic responses. A third possibility is that decisions emerge from the interplay of multiple decision systems (McClure et al. 2004). The scheme of **Figure 1** is somewhat intermediate. Indeed, I posit the existence of a unitary representation of value, which integrates sensory stimuli and motivational states. In turn, values inform emotional and autonomic responses. More work is necessary to clarify the relation between motivation, emotion, and autonomic responses.

## CONCLUSIONS

I have reviewed current knowledge on the neural mechanisms of economic choice and, more specifically, on how values are computed, represented, and compared when individuals make a choice. I have also presented a good-based model that provides a unifying framework and accounts for current results. Finally, I have discussed open issues that should be examined in the future.

Much work in the past few years was designed to test the hypothesis that, while making choices, individuals indeed assign subjective values to the available goods. This proposition has now been successfully tested with respect to a variety of determinants: commodity, quantity, risk, delay, effort, and others. Although other determinants remain to be examined, current evidence affords the provisional conclusion that economic values are indeed represented at the neuronal level. This conclusion might appear deceptively foreknown. In fact, a concept of value rooted in neural evidence is a paradigmatic step forward compared with how values have been conceptualized in

the past century. Indeed, both behaviorism and neoclassical economics—arguably the dominant theories of choice in psychology and economics since the 1930s—explicitly state that values are purely descriptive entities, not

mental states. For this reason, the demonstration that economic values are neurally and thus psychologically real entities may be regarded as a major success for the emerging field of neuroeconomics.

### SUMMARY POINTS

1. Different types of decision (perceptual decisions, economic choice, action selection, etc.) involve different mental operations and different brain mechanisms. Economic choice involves assigning values to different goods and comparing these values.
2. Measuring the neural representation of economic value requires letting subjects choose between different options, inferring subjective values from the indifference point, and using that measure to analyze neural activity.
3. A representation of economic value is abstract if neural activity does not depend on the sensorimotor contingencies of choice and if the representation is domain-general. Such an abstract representation exists in the OFC and vmPFC. Lesions to these areas specifically disrupt economic choice behavior.
4. The representation of value in the OFC is menu invariant: Values assigned to different goods are independent of one another. Menu invariance implies preference transitivity.
5. Values computed in different behavioral conditions may vary substantially. The representation of value in the OFC is range adapting: A given range of neural activity represents different value ranges in different behavioral conditions.
6. While computing the value of a given good, subjects integrate a variety of determinants. Some determinants may be learned, whereas other determinants may not be learned. Thus values are computed online at the time of choice.
7. A neural representation of action values may contribute to economic choice if three conditions are met: Neural activity must be genuinely motor, neural activity must be modulated by subjective value, and neural activity must not be downstream of the decision.
8. In addition to guiding an action, values and choice outcomes inform a variety of cognitive and neural systems, including sensory and motor systems (through perceptual attention and attention-like mechanisms), learning (e.g., through mechanisms of reinforcement learning), and emotion (including autonomic functions).

### FUTURE ISSUES

1. Where in the brain are different determinants of value (e.g., risk, cost, delay) computed, and how are they represented?
2. The process of integrating multiple determinants into a value signal can be thought of as analogous to computing a nonlinear function with many arguments. How is this computation implemented at the neuronal level? Can it be captured with a computational model?

3. Through which neuronal mechanisms are different values compared to make a decision? Are the underlying algorithms similar to those observed in other brain systems?
4. Assuming that choices indeed take place in goods space, through which neuronal mechanisms is a choice outcome transformed into an action plan?
5. In the OFC and other areas, neurons may encode values in a positive or negative way (i.e., the encoding slope may be positive or negative). Do these two neuronal populations play different roles in choice behavior?
6. Abstract representations of value appear to exist in the primate OFC and vmPFC, but the relative contributions of these two brain regions to choice behavior are not clear. In fact, the anatomical connectivity of the orbital network and medial network is markedly different. How do OFC and vmPFC contribute to economic choices?
7. No abstract representation of value has yet been found in the rodent OFC—a striking difference with primates. Possible reasons for this discrepancy include a poor homology between “OFC” as defined in different species, the hypothesis that an abstract representation of value may have emerged late in evolution, and differences in experimental procedures. How can differences among species be explained best?
8. Choice traits such as temporal discounting, risk aversion, and loss aversion ultimately affect subjective values. Thus their neuronal correlates may be and have been observed by measuring neural activity encoding subjective value. However, these measures generally do not explain the neurobiological origin of these choice traits. Can temporal discounting and other choice traits be explained as the result of specific neuronal properties?

## DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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## LITERATURE CITED

- Adams CD. 1982. Variations in the sensitivity of instrumental responding to reinforcer devaluation. *Q. J. Exp. Psych.* 34B:77–98
- Adams CD, Dickinson A. 1981. Instrumental responding following reinforcer devaluation. *Q. J. Exp. Psych.* 33B:109–21
- Amador N, Schlag-Rey M, Schlag J. 2000. Reward-predicting and reward-detecting neuronal activity in the primate supplementary eye field. *J. Neurophysiol.* 84:2166–70
- Balleine BW, Dickinson A. 1998. Goal-directed instrumental action: contingency and incentive learning and their cortical substrates. *Neuropharmacology* 37:407–19
- Balleine BW, Ostlund SB. 2007. Still at the choice-point: action selection and initiation in instrumental conditioning. *Ann. N.Y. Acad. Sci.* 1104:147–71

- Baxter MG, Gaffan D, Kyriazis DA, Mitchell AS. 2009. Ventrolateral prefrontal cortex is required for performance of a strategy implementation task but not reinforcer devaluation effects in rhesus monkeys. *Eur. J. Neurosci.* 29:2049–59
- Bennur S, Gold JI. 2011. Distinct representations of a perceptual decision and the associated oculomotor plan in the monkey lateral intraparietal area. *J. Neurosci.* 31:913–21
- Berlin HA, Rolls ET, Kischka U. 2004. Impulsivity, time perception, emotion and reinforcement sensitivity in patients with orbitofrontal cortex lesions. *Brain* 127:1108–26
- Brooks AM, Pammi VS, Noussair C, Capra CM, Engelmann JB, Berns GS. 2010. From bad to worse: striatal coding of the relative value of painful decisions. *Front. Neurosci.* 4:176
- Bundesden C. 1990. A theory of visual attention. *Psychol. Rev.* 97:523–47
- Cai X, Kim S, Lee D. 2011. Heterogeneous coding of temporally discounted values in the dorsal and ventral striatum during intertemporal choice. *Neuron* 69:170–82
- Cai X, Padoa-Schioppa C. 2010. Dissociating economic choice from action selection. *Soc. Neurosci. Meet. Plann. Abstr.* 813.1
- Camerer C. 2003. *Behavioral Game Theory: Experiments in Strategic Interaction*. Princeton, NJ: Russell Sage Found., Princeton Univ. Press
- Christopoulos GI, Tobler PN, Bossaerts P, Dolan RJ, Schultz W. 2009. Neural correlates of value, risk, and risk aversion contributing to decision making under risk. *J. Neurosci.* 29:12574–83
- Cisek P, Kalaska JF. 2002. Simultaneous encoding of multiple potential reach directions in dorsal premotor cortex. *J. Neurophysiol.* 87:1149–54
- Colwill RM, Rescorla RA. 1986. Associative structures in instrumental conditioning. In *The Psychology of Learning and Motivation*, ed. GH Bower, pp. 55–104. Orlando, FL: Academic
- Critchley HD. 2005. Neural mechanisms of autonomic, affective, and cognitive integration. *J. Comp. Neurol.* 493:154–66
- Damasio AR. 1994. *Descartes' Error: Emotion, Reason, and the Human Brain*. New York: Putnam. xix, 312 pp.
- De Martino B, Kumaran D, Holt B, Dolan RJ. 2009. The neurobiology of reference-dependent value computation. *J. Neurosci.* 29:3833–42
- Dorris MC, Glimcher PW. 2004. Activity in posterior parietal cortex is correlated with the relative subjective desirability of action. *Neuron* 44:365–78
- Feierstein CE, Quirk MC, Uchida N, Sosulski DL, Mainen ZF. 2006. Representation of spatial goals in rat orbitofrontal cortex. *Neuron* 51:495–507
- Fellows LK, Farah MJ. 2007. The role of ventromedial prefrontal cortex in decision making: judgment under uncertainty or judgment per se? *Cereb. Cortex* 17:2669–74
- FitzGerald TH, Seymour B, Dolan RJ. 2009. The role of human orbitofrontal cortex in value comparison for incommensurable objects. *J. Neurosci.* 29:8388–95
- Frederick S, Loewenstein G, O'Donoghue T. 2002. Time discounting and time preference: a critical review. *J. Econ. Lit.* 40:351–401
- Fredrikson M, Furmark T, Olsson MT, Fischer H, Andersson J, Langstrom B. 1998. Functional neuroanatomical correlates of electrodermal activity: a positron emission tomographic study. *Psychophysiology* 35:179–85
- Gallagher M, McMahan RW, Schoenbaum G. 1999. Orbitofrontal cortex and representation of incentive value in associative learning. *J. Neurosci.* 19:6610–14
- Glimcher PW. 2008. Choice: towards a standard back-pocket model. See Glimcher et al. 2008, pp. 501–19
- Glimcher PW, Camerer CF, Fehr E, Poldrack RA. 2008. *Neuroeconomics: Decision Making and the Brain*. Amsterdam: Elsevier. 538 pp.
- Glimcher PW, Dorris MC, Bayer HM. 2005. Physiological utility theory and the neuroeconomics of choice. *Games Econ. Behav.* 52:213–56
- Gold JI, Shadlen MN. 2003. The influence of behavioral context on the representation of a perceptual decision in developing oculomotor commands. *J. Neurosci.* 23:632–51
- Grace RC. 1993. Violations of transitivity: implications for a theory of contextual choice. *J. Exp. Anal. Behav.* 60:185–201
- Grattan LE, Glimcher PW. 2010. No evidence for spatial tuning in orbitofrontal cortex. *Soc. Neurosci. Meet. Plann. Abstr.* 102.23



- Gregorios-Pippas L, Tobler PN, Schultz W. 2009. Short-term temporal discounting of reward value in human ventral striatum. *J. Neurophysiol.* 101:1507–23
- Horwitz GD, Batista AP, Newsome WT. 2004. Representation of an abstract perceptual decision in macaque superior colliculus. *J. Neurophysiol.* 91:2281–96
- Hsu M, Bhatt M, Adolphs R, Tranel D, Camerer CF. 2005. Neural systems responding to degrees of uncertainty in human decision-making. *Science* 310:1680–83
- Hsu M, Krajbich I, Zhao C, Camerer CF. 2009. Neural response to reward anticipation under risk is nonlinear in probabilities. *J. Neurosci.* 29:2231–37
- Ikeda T, Hikosaka O. 2003. Reward-dependent gain and bias of visual responses in primate superior colliculus. *Neuron* 39:693–700
- Izquierdo A, Suda RK, Murray EA. 2004. Bilateral orbital prefrontal cortex lesions in rhesus monkeys disrupt choices guided by both reward value and reward contingency. *J. Neurosci.* 24:7540–48
- Kable JW, Glimcher PW. 2007. The neural correlates of subjective value during intertemporal choice. *Nat. Neurosci.* 10:1625–33
- Kable JW, Glimcher PW. 2009. The neurobiology of decision: consensus and controversy. *Neuron* 63:733–45
- Kahneman D, Tversky A. 1979. Prospect theory: an analysis of decision under risk. *Econometrica* 47:263–91
- Kahneman D, Tversky A, eds. 2000. *Choices, Values and Frames*. Cambridge, UK/New York: Russell Sage Found./Cambridge Univ. Press. xx, 840 pp.
- Kalenscher T, Tobler PN, Huijbers W, Daselaar SM, Pennartz CM. 2010. Neural signatures of intransitive preferences. *Front. Hum. Neurosci.* 4:49
- Kawagoe R, Takikawa Y, Hikosaka O. 1998. Expectation of reward modulates cognitive signals in the basal ganglia. *Nat. Neurosci.* 1:411–16
- Kazama A, Bachevalier J. 2009. Selective aspiration or neurotoxic lesions of orbital frontal areas 11 and 13 spared monkeys' performance on the object discrimination reversal task. *J. Neurosci.* 29:2794–804
- Kennerley SW, Dahmubed AF, Lara AH, Wallis JD. 2009. Neurons in the frontal lobe encode the value of multiple decision variables. *J. Cogn. Neurosci.* 21:1162–78
- Kennerley SW, Wallis JD. 2009. Encoding of reward and space during a working memory task in the orbitofrontal cortex and anterior cingulate sulcus. *J. Neurophysiol.* 102:3352–64
- Kennerley SW, Walton ME, Behrens TE, Buckley MJ, Rushworth MF. 2006. Optimal decision making and the anterior cingulate cortex. *Nat. Neurosci.* 9:940–47
- Kim H, Sul JH, Huh N, Lee D, Jung MW. 2009. Role of striatum in updating values of chosen actions. *J. Neurosci.* 29:14701–12
- Kim S, Hwang J, Lee D. 2008. Prefrontal coding of temporally discounted values during intertemporal choice. *Neuron* 59:161–72
- Kimmel DL, Rangel A, Newsome WT. 2010. Value representations in the primate orbitofrontal cortex during cost-benefit decision making. *Soc. Neurosci. Meet. Plann. Abstr.* 129.14
- Klein JT, Deaner RO, Platt ML. 2008. Neural correlates of social target value in macaque parietal cortex. *Curr. Biol.* 18:419–24
- Kobayashi S, Pinto de Carvalho O, Schultz W. 2010. Adaptation of reward sensitivity in orbitofrontal neurons. *J. Neurosci.* 30:534–44
- Kobayashi S, Schultz W. 2008. Influence of reward delays on responses of dopamine neurons. *J. Neurosci.* 28:7837–46
- Koenigs M, Tranel D. 2007. Irrational economic decision-making after ventromedial prefrontal damage: evidence from the Ultimatum Game. *J. Neurosci.* 27:951–56
- Kreps DM. 1990. *A Course in Microeconomic Theory*. Princeton, NJ: Princeton Univ. Press. 850 pp.
- Lau B, Glimcher PW. 2008. Value representations in the primate striatum during matching behavior. *Neuron* 58:451–63
- Leon MI, Shadlen MN. 1999. Effect of expected reward magnitude on the response of neurons in the dorso-lateral prefrontal cortex of the macaque. *Neuron* 24:415–25
- Levy I, Snell J, Nelson AJ, Rustichini A, Glimcher PW. 2010. Neural representation of subjective value under risk and ambiguity. *J. Neurophysiol.* 103:1036–47
- Louie K, Glimcher PW. 2010. Separating value from choice: delay discounting activity in the lateral intraparietal area. *J. Neurosci.* 30:5498–507

- Machado CJ, Bachevalier J. 2007a. The effects of selective amygdala, orbital frontal cortex or hippocampal formation lesions on reward assessment in nonhuman primates. *Eur. J. Neurosci.* 25:2885–904
- Machado CJ, Bachevalier J. 2007b. Measuring reward assessment in a semi-naturalistic context: the effects of selective amygdala, orbital frontal or hippocampal lesions. *Neuroscience* 148:599–611
- Matsumoto K, Suzuki W, Tanaka K. 2003. Neuronal correlates of goal-based motor selection in the prefrontal cortex. *Science* 301:229–32
- Maunsell JH. 2004. Neuronal representations of cognitive state: reward or attention? *Trends Cogn. Sci.* 8:261–65
- McClure SM, Laibson DI, Loewenstein G, Cohen JD. 2004. Separate neural systems value immediate and delayed monetary rewards. *Science* 306:503–7
- McCoy AN, Crowley JC, Haghighian G, Dean HL, Platt ML. 2003. Saccade reward signals in posterior cingulate cortex. *Neuron* 40:1031–40
- Minamimoto T, Hori Y, Kimura M. 2005. Complementary process to response bias in the centromedian nucleus of the thalamus. *Science* 308:1798–801
- Mobini S, Body S, Ho MY, Bradshaw CM, Szabadi E, et al. 2002. Effects of lesions of the orbitofrontal cortex on sensitivity to delayed and probabilistic reinforcement. *Psychopharmacology (Berl.)* 160:290–98
- Montague PR, King-Casas B, Cohen JD. 2006. Imaging valuation models in human choice. *Annu. Rev. Neurosci.* 29:417–48
- Morrison SE, Salzman CD. 2009. The convergence of information about rewarding and aversive stimuli in single neurons. *J. Neurosci.* 29:11471–83
- O'Neill M, Schultz W. 2010. Coding of reward risk by orbitofrontal neurons is mostly distinct from coding of reward value. *Neuron* 68:789–800
- Ongur D, Price JL. 2000. The organization of networks within the orbital and medial prefrontal cortex of rats, monkeys and humans. *Cereb. Cortex* 10:206–19
- Padoa-Schioppa C. 2007. Orbitofrontal cortex and the computation of economic value. *Ann. N.Y. Acad. Sci.* 1121:232–53
- Padoa-Schioppa C. 2009. Range-adapting representation of economic value in the orbitofrontal cortex. *J. Neurosci.* 29:14004–14
- Padoa-Schioppa C, Assad JA. 2006. Neurons in orbitofrontal cortex encode economic value. *Nature* 441:223–26
- Padoa-Schioppa C, Assad JA. 2008. The representation of economic value in the orbitofrontal cortex is invariant for changes of menu. *Nat. Neurosci.* 11:95–102
- Peters J, Buchel C. 2009. Overlapping and distinct neural systems code for subjective value during intertemporal and risky decision making. *J. Neurosci.* 29:15727–34
- Picard N, Strick PL. 2001. Imaging the premotor areas. *Curr. Opin. Neurobiol.* 11:663–72
- Pickens CL, Saddoris MP, Setlow B, Gallagher M, Holland PC, Schoenbaum G. 2003. Different roles for orbitofrontal cortex and basolateral amygdala in a reinforcer devaluation task. *J. Neurosci.* 23:11078–84
- Pine A, Seymour B, Roiser JP, Bossaerts P, Friston KJ, et al. 2009. Encoding of marginal utility across time in the human brain. *J. Neurosci.* 29:9575–81
- Plassmann H, O'Doherty J, Rangel A. 2007. Orbitofrontal cortex encodes willingness to pay in everyday economic transactions. *J. Neurosci.* 27:9984–88
- Popper K. 1963. Science: conjectures and refutations. In *Conjectures and Refutations*, pp. 43–86. London/New York: Routledge Classics
- Price JL. 1999. Prefrontal cortical networks related to visceral function and mood. *Ann. N.Y. Acad. Sci.* 877:383–96
- Price JL, Drevets WC. 2010. Neurocircuitry of mood disorders. *Neuropsychopharmacology* 35:192–216
- Rahman S, Sahakian BJ, Hodges JR, Rogers RD, Robbins TW. 1999. Specific cognitive deficits in mild frontal variant of frontotemporal dementia. *Brain* 122(Pt. 8):1469–93
- Rangel A, Camerer C, Montague PR. 2008. A framework for studying the neurobiology of value-based decision making. *Nat. Rev. Neurosci.* 9:545–56
- Rangel A, Hare T. 2010. Neural computations associated with goal-directed choice. *Curr. Opin. Neurobiol.* 20:262–70

- Roesch MR, Olson CR. 2003. Impact of expected reward on neuronal activity in prefrontal cortex, frontal and supplementary eye fields and premotor cortex. *J. Neurophysiol.* 90:1766–89
- Roesch MR, Olson CR. 2005. Neuronal activity in primate orbitofrontal cortex reflects the value of time. *J. Neurophysiol.* 94:2457–71
- Roesch MR, Taylor AR, Schoenbaum G. 2006. Encoding of time-discounted rewards in orbitofrontal cortex is independent of value representation. *Neuron* 51:509–20
- Rudebeck PH, Behrens TE, Kennerley SW, Baxter MG, Buckley MJ, et al. 2008. Frontal cortex subregions play distinct roles in choices between actions and stimuli. *J. Neurosci.* 28:13775–85
- Rudebeck PH, Walton ME, Smyth AN, Bannerman DM, Rushworth MF. 2006. Separate neural pathways process different decision costs. *Nat. Neurosci.* 9:1161–68
- Rushworth MF, Mars RB, Summerfield C. 2009. General mechanisms for making decisions? *Curr. Opin. Neurobiol.* 19:75–83
- Samejima K, Ueda Y, Doya K, Kimura M. 2005. Representation of action-specific reward values in the striatum. *Science* 310:1337–40
- Schoenbaum G, Roesch MR, Stalnaker TA, Takahashi YK. 2009. A new perspective on the role of the orbitofrontal cortex in adaptive behaviour. *Nat. Rev. Neurosci.* 10:885–92
- Seo H, Lee D. 2007. Temporal filtering of reward signals in the dorsal anterior cingulate cortex during a mixed-strategy game. *J. Neurosci.* 27:8366–77
- Seymour B, McClure SM. 2008. Anchors, scales and the relative coding of value in the brain. *Curr. Opin. Neurobiol.* 18:173–78
- Shafir S. 2002. Context-dependent violations of rational choice in honeybees (*Apis mellifera*) and gray jays (*Perisoreus canadensis*). *Behav. Ecol. Sociobiol.* 51:180–87
- Shenhav A, Greene JD. 2010. Moral judgments recruit domain-general valuation mechanisms to integrate representations of probability and magnitude. *Neuron* 67:667–77
- Shidara M, Richmond BJ. 2002. Anterior cingulate: single neuronal signals related to degree of reward expectancy. *Science* 296:1709–11
- Skinner BF. 1953. *Science and Human Behavior*. New York: Macmillan. 461 pp.
- Sloan J, Kennerley SW, Wallis JD. 2010. Neural encoding of cost-based decisions: effort versus delay. *Soc. Neurosci. Meet. Plann. Abstr.* 805.16
- Sugrue LP, Corrado GS, Newsome WT. 2004. Matching behavior and the representation of value in the parietal cortex. *Science* 304:1782–87
- Sutton RS, Barto AG. 1998. *Reinforcement Learning: An Introduction*. Cambridge, MA: MIT Press. xviii, 322 pp.
- Thevarajah D, Webb R, Ferrall C, Dorris MC. 2010. Modeling the value of strategic actions in the superior colliculus. *Front. Behav. Neurosci.* 3:57
- Tversky A. 1969. The intransitivity of preferences. *Psychol. Rev.* 76:31–48
- Tversky A, Shafir E. 2004. *Preference, Belief, and Similarity: Selected Writings*. Cambridge, MA: MIT Press. xvi, 1023 pp.
- Tversky A, Simonson I. 1993. Context-dependent preferences. *Manag. Sci.* 39:117–85
- van Duuren E, Escamez FA, Joosten RN, Visser R, Mulder AB, Pennartz CM. 2007. Neural coding of reward magnitude in the orbitofrontal cortex of the rat during a five-odor olfactory discrimination task. *Learn. Mem.* 14:446–56
- Walton ME, Bannerman DM, Rushworth MF. 2002. The role of rat medial frontal cortex in effort-based decision making. *J. Neurosci.* 22:10996–1003
- Watson KK, Platt ML. 2008. Orbitofrontal neurons encode both social and nonsocial rewards. *Soc. Neurosci. Meet. Plann. Abstr.* 691.11
- Williams ZM, Eskandar EN. 2006. Selective enhancement of associative learning by microstimulation of the anterior caudate. *Nat. Neurosci.* 9:562–68
- Winstanley CA, Theobald DE, Cardinal RN, Robbins TW. 2004. Contrasting roles of basolateral amygdala and orbitofrontal cortex in impulsive choice. *J. Neurosci.* 24:4718–22
- Wise SP. 2008. Forward frontal fields: phylogeny and fundamental function. *Trends Neurosci.* 31:599–608
- Wunderlich K, Rangel A, O'Doherty JP. 2010. Economic choices can be made using only stimulus values. *Proc. Natl. Acad. Sci. USA* 107:15005–10

- Zald DH. 2006. The rodent orbitofrontal cortex gets time and direction. *Neuron* 51:395–97
- Ziegler G, Dahnke R, Yeragani VK, Bar KJ. 2009. The relation of ventromedial prefrontal cortex activity and heart rate fluctuations at rest. *Eur. J. Neurosci.* 30:2205–10

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- Niehans J. 1990. *A History of Economic Theory: Classic Contributions, 1720–1980*. Baltimore, MD: Johns Hopkins Univ. Press. 578 pp.
- Padoa-Schioppa C. 2008. The syllogism of neuro-economics. *Econ. Philos.* 24:449–57
- Ross D. 2005. *Economic Theory and Cognitive Science: Microexplanation*. Cambridge, MA: MIT Press. 444 pp.