Neuronal Representations of Value
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INTRODUCTION

Value and Decision-making in Evolutionary Perspective

Humans continuously engage in behaviors that entail a choice. For example, economic choice – the choice between different goods – takes place when people buy groceries, select a pension plan, or choose a spouse. Choices also take place in the perceptual and motor domains. For example, in the presence of ambiguous sensory stimuli, a particular percept can be thought of as the result of a choice process (Gold and Shadlen, 2001). Moreover, perceptual attention – the selection of one particular stimulus to which processing resources are preferentially allocated – can also be described as the result of a choice process. In the motor domain, enacting an abstract plan (e.g., "pick an apple") entails selecting one particular action (e.g., "reach with the left hand") out of many suitable actions, which implies a choice.

The brain systems that generate such choices originally evolved to promote behaviors that enhance biological fitness, such as acquiring food and shelter, attracting mates, avoiding predators, and prevailing over competitors. Thus, the nervous system comprises a suite of morphological and behavioral adaptations for surmounting specific environmental and social challenges. Both theoretical and empirical studies in animals support the idea that, to the limits of physiological and cognitive constraints, behavioral choices serve to optimize evolutionary fitness and thus can be viewed as economical. Accordingly, brains appear to be exquisitely specialized to attend to key features of the environment, determine the predictive value of these features, and then use this information to compute the optimal behavioral choice. Economic concepts such as "value" and "optimality" thus provide a broad framework to describe different kinds of choice behavior.

Rewards can be considered proximate goals that, when acquired, tend to enhance survival and reproductive success. Similarly, avoiding punishment is a proximate goal that ultimately serves to enhance the long-term likelihood of survival and reproduction. These definitions extend the traditional psychological and neurobiological notions of reward and punishment, which are typically defined by the quality of eliciting approach and avoidance. Although still in the early stages, the convergence of concepts and experimental approaches from economics, psychology, and neuroscience – the emerging field of neuroeconomics – offers a potentially powerful way to study the neural mechanisms underlying reward, punishment, and decision-making. In the long run, this might also advance our understanding of the dysfunction of these systems in mental disorders like schizophrenia, pathological risk-taking, and drug addiction. We contend that understanding of the neurobiological basis of decision-making will be deepened by studying the economic problems solved by people and animals in their natural physical and social environments using neurophysiological, neuroimaging, and neuropharmacological techniques in the laboratory. We also suggest that studies of reward, punishment, and decision-making in non-human primates will be particularly instructive, given the many biological and behavioral homologies shared by these species and humans.

In this chapter, we review the current understanding of the neural processes that construct representations of biologically-relevant value, translate these valuation signals into behavioral decisions, and update representations of value upon which future decisions are made. These results are derived from studies where the activity of single neurons is recorded in monkeys making choices. Our review will focus in particular on three brain regions – the orbitofrontal cortex (OFC), the lateral intraparietal area (LIP), and the posterior cingulate cortex (CGp). Value representations differ substantially in these brain areas, suggesting that distinct representation of value may contribute to distinct decision processes.

ECONOMIC CHOICE AND THE ORBITOFRONTAL CORTEX

Lesion, Neuroimaging, and Single-cell Studies of OFC and Decision-making

Consider a person sitting in a restaurant and choosing from the menu between tuna tartare and fried calamari. Presumably, the person assigns a value to the tuna and a value to the calamari, and then compares the two values to make a decision (Padoa-Schioppa et al., 2006). Economic choice – the choice between different goods – thus entails assigning values to the available options. In this section, we review evidence indicating that neurons in the OFC encode the value subjects assign to the available goods during economic choice.

A strong link between economic choice and the OFC comes from observations of patients with brain damage in this area, who present choice deficits in multiple domains. For example, early clinical signs of fronto-temporal dementia (FTD, a neurodegenerative disorder that initially affects the orbital cortex and parts of the temporal lobe) include eating disorders.
In other words, FTD patients seem to assign the “wrong value” to appetitive stimuli (Pasquier and Petit, 1997). Patients with OFC lesions also display abnormal behavior in gambling tasks (Bechara et al., 1999; Rahman et al., 1994), suggesting a difficulty in coping with risk. However, choice deficits are also apparent in simple preference judgment tasks, in which patients with OFC lesions make inconsistent or erratic choices significantly more often than do either healthy subjects or patients with dorsolateral frontal lesions (Fellows and Farah, 2007). Finally, OFC patients also display unusual or poor choice patterns in the ultimatum game (Koenigs and Tranel, 2007) and in social contexts, as famously noted in the case of Phineas Gage (Damasio et al., 1994).

A second strong link between economic choice behavior and OFC comes from imaging experiments in humans. Many studies found higher activation in the OFC when subjects were presented with pleasant stimuli in multiple sensory modalities (e.g., visual, taste, etc.) compared to neutral stimuli (O’Doherty, 2004). Most interestingly, in experiments that compared conditions in which subjects did or did not make a choice, OFC was significantly more active in the choice condition (Arana et al., 2003). The same area was also more activated by high incentives compared to low incentives. In comparison, neural activation in the amygdala varied depending on the incentive level, but did not vary with task demands.

Classical results of single-cell recordings in non-human primates are also consistent with the hypothesis that OFC neurons might be a substrate for economic valuation. For example, in an early study, Thorpe and colleagues (1983) observed that neurons in OFC responded to the presentation of visual stimuli in a way that was not purely “sensory.” The response of one neuron to the visual presentation of a liquid-filled syringe depended on whether in previous trials the liquid was apple juice or salted water, even though the syringe was visually indistinguishable in the two conditions. Rolls and colleagues (1989) subsequently found that the activity of OFC neurons in response to a particular taste could be altered by hunger and satiety, a modulation not observed in the primary taste area. These studies thus indicated that the activity of OFC neurons is sensitive to both the nature of physical stimulation and motivational state. More recently, Wallis and colleagues found that the activity of neurons in OFC can be modulated by the amount of juice delivered to the monkey (Wallis, 2007). Roesch and Olson (2005) observed that OFC neuronal activity varied depending on the duration of a time delay intervening before juice delivery. Interestingly, there was an inverse correlation between the effects of juice amount and the effects of time delay. Under the assumption that the neurons recorded in that study encode the subjective value at stake in any trial, one possible interpretation of this result is that the delay represents a cost for the monkey (for example due to discounting) and that OFC neurons encode net value (benefit–cost).

Neurons in OFC Encode Economic Value

Taken together, these results suggest that neurons in OFC may represent the behavioral valence of goods. However, in the experiments with monkeys described above, the animals were never asked to choose based on their own preferences. Rather, monkeys were either simply delivered juice, or they were asked to select between two options, one of which was always objectively advantageous (i.e., stochastically dominant). Consequently, these tasks could not provide a measure of the subjective value monkeys assigned to the juice. In contrast, the behavioral paradigm illustrated in Figure 29.1 provides such a measure (Padoa-Schioppa and Assad, 2006). In this experiment, thirsty monkeys chose between two different juices offered in variable amounts. When the two juices were offered in equal amounts, monkeys had a strong preference for one of the juices. However, if the other, less preferred juice was offered in sufficiently large amounts, monkeys chose it. The relative value of the two juices could thus be inferred from the indifference point – the quantity ratio at which monkeys chose either juice equally often.

In a recent study, Padoa-Schioppa and Assad used this behavioral paradigm to examine the activity of neurons in OFC as a function of subjective value (Padoa-Schioppa and Assad, 2006). Figure 29.2 illustrates the activity of one representative cell. In this session, the monkey chose between grape juice (A) and diluted cranberry juice (B). The behavioral choice pattern (Figure 29.2a, black symbols) indicated that V(A) = 3.0V(B). The response of the neuron (Figure 29.2a, red symbols) showed a characteristic U-shape, similar to what would be expected if the neuron encoded the value chosen by the monkey in any given trial. Indeed, the activity of the neuron was low when the monkey chose 1A or when it chose 3B (in units of V(B), chosen value = 3); the neuronal activity was highest when the monkey chose 3A and when it chose 1B (chosen value ≈ 10). This point can best be appreciated in Figure 29.2b, where the activity of the neuron (y-axis) is plotted directly against the variable chosen value (x-axis). A further analysis confirms that U-shaped responses like these encode the subjective value monkeys assign.
In fact, the identity of neuronal activity encodes the chosen value leads to a simple prediction regarding slopes \( a_A \) and \( a_B \). Specifically, \( a_A \) should be proportional to the value of \( A \), \( a_B \) should be proportional to the value of \( B \), and the ratio \( k^* = a_A / a_B \) should be equal to the value ratio \( V(A)/V(B) \). In other words, the slope ratio \( k^* \) provides a neuronal measure of the relative value of the two juices, independent of the behavioral measure of relative value \( n^* \), which represents the indifference point obtained from the sigmoid fit. If U-shaped responses indeed encode the chosen value, the identity \( k^* = n^* \) should hold true. This condition is satisfied for the cell in Figure 2, for which the neuronal measure of relative value \( k^* = 2.8(\pm0.7) \) is statistically indistinguishable from the behavioral measure \( n^* = 3.0 \). In fact, the identity \( k^* = n^* \) holds true in general. Considering the entire population, a linear regression provides \( k^* = -0.13(\pm0.15) + 1.05(\pm0.15)n^* \) (average across 10 juice pairs), which is statistically indistinguishable from \( k^* = n^* \). This result demonstrates that U-shaped responses indeed encode value as a subjective quantity, as opposed to any physical property of the juices. Indeed, if U-shaped responses encoded a physical property of the juices (e.g., sugar content), U-shapes should not vary from session to session depending on the relative value the monkey assigns to the juices in that particular session. In other words, \( k^* \) should be independent of \( n^* \) across behavioral sessions, contrary to what is observed. Hence, U-shaped responses encode the value monkeys assign to the juice they choose to consume (Roesch and Olson, 2005).

Neurons encoding the chosen value were frequent in OFC, but other types of neuronal responses were also found. For example, OFC neurons often encoded the offer value – that is, the value of one of the two juices alone. Figure 29.3 (a and b) shows the activity of two neurons encoding, respectively, offer value \( A \) and offer value \( B \). Other frequently observed responses varied in a binary fashion depending on the type of juice chosen by the monkey, independently of the amount (Figure 29.3c). These responses appear to encode the juice taste.

One fundamental aspect of the value representation in OFC is that neuronal responses in this area do not depend on the visuo-motor contingencies of choice. This point can be observed in Figure 29.2d, where the activity of the same neuron shown in Figure 29.2a is plotted separately for trials in which the monkey indicated its choice with an eye movement to the left (red) or to the right (green). The activity was nearly identical for the two groups of trials. In other words, this neuron encoded the value of the chosen juice per se, independently of the action used by the monkey to indicate its choice. Similarly, the activity of this cell did not depend on the spatial configuration of the stimuli on the monitor (i.e., whether juice \( A \) was offered on the right and juice \( B \) on the left, or vice versa). The same was true across the population. For more than 95% of neurons in OFC, the activity was independent of the visuo-motor contingencies of choice.

V. THE NEURAL MECHANISMS FOR CHOICE

![Figure 29.1](image-url)
As described in the following sections, the observation that neurons in OFC represent value independently of the sensory-motor contingencies of choice fundamentally distinguishes this representation of value from that found in other brain areas in monkeys. Interestingly, this characteristic also seems to distinguish OFC responses in primates and rodents. Indeed, two recent studies found that neuronal activity in the rat OFC actually does depend on sensory and motor contingencies (Feierstein et al., 2006). One possibility is that the region examined in rats was not homologous to the region examined in monkeys. Alternatively, it is possible that an abstract representation of value removed from sensory and motor contingencies emerged subsequent to the divergence of primates and rodents from a common ancestor (Roesch et al., 2006).

**The Representation of Value in OFC is Invariant for Changes of Menu**

For any neuronal representation of value, a broad and fundamental question is whether and how value-encoding neuronal responses depend on the behavioral context. In principle, two ways in which the
behavioral context might change can be distinguished. Changes of “menu” are moment-to-moment changes in the available options. For example, if a person in a wine store compares serially different pairs of bottles, changes from one pair-wise comparison to the next are changes of menu. From a computational point of view, a valuation system invariant for changes of menu presents clear advantages, because it guarantees stable choices and preference transitivity (see Box 29.1).

In contrast, changes of “condition” (including changes of the chooser’s internal state) are changes that occur on a longer timescale. For example, if that same person goes from the wine store (where different options cost about $15) to a car retailer (where different options cost $15,000 or more), his valuation system might adapt to the new range of values. Similarly, the valuation system could also adapt to changes of internal motivation.

In a second study, Padoa-Schioppa and Assad (2008) examined specifically whether the representation of value in OFC depends on the menu – that is,

Transitivity is a fundamental trait of economic choice behavior. Given three options, X, Y, and Z, if an individual prefers X to Y and Y to Z, she ought to prefer X to Z (preference transitivity). Likewise, if an individual is indifferent between X and Y and between Y and Z, she ought to be indifferent between X and Z (indifference transitivity). We indicate with \( n_{X:Y} \) the relative value of X and Y, such that \( V(X) = n_{X:Y} V(Y) \). Under the assumption of linear indifference curves (i.e., if value functions for different goods are all the same up to a scaling factor), indifference transitivity reduces to the relationship \( n_{A:B} = n_{B:C} n_{A:C} \) (value transitivity) (Padoa-Schioppa and Assad, 2008).
whether neuronal responses encoding the value of one particular good depend on what other goods are available at the same time. In this case, monkeys chose between three juices (A, B, and C, in decreasing order of preference). In each trial, monkeys chose between two juices, and trials with the three juice pairs (A:B, B:C, and C:A) were randomly interleaved. For example, in the session illustrated in Figure 29.4a, a monkey chose between grape juice (A), fruit punch (B), and apple juice (C). The three panels in the figure refer, respectively, to trials A:B, B:C and C:A, and black symbols represent the choice patterns. Notably, the three relative values obtained from the sigmoid fit combine according to value transitivity, in the sense that 1.4 * 1.9 ≈ 2.6. The values monkeys assigned to different goods satisfied transitivity in general (Figure 29.4b). As a consequence, quantities of the three juices could be expressed on the same value scale.

Padoa-Schioppa and Assad found that neuronal responses in OFC were typically invariant for changes of menu. For example, the activity of the cell illustrated in Figure 29.4a (red symbols) encoded the \textit{chosen value} independently of the juice pair. Value transitivity across sessions. Each data point in the scatter plot represents one session, and all 124 sessions are shown. For each session, gray error bars represent the errors of measure (s.d.). The diagonal dashed line corresponds to $n_{A:C} = n_{A:B} \times n_{B:C}$. Relative values measured in any given session satisfy transitivity unless they are significantly removed from this line. Value transitivity was satisfied by all 124 sessions ($P > 0.05$). (c) Same neuronal response as in (a), combining data from the three juice pairs. The firing rate (y-axis) is plotted against the variable \textit{chosen value} (x-axis) and the three colors represent the three juice pairs. The three regression lines (from an analysis of covariance (ANCOVA)) are statistically indistinguishable from one another, indicating that the activity of the cell encodes the \textit{chosen value} independently of the menu. Similarly, the activity of neurons encoding the \textit{offer value} or the taste of one particular juice did not
Ordinality, Cardinality and Neuronal Adaptation

At first glance, the results illustrated in Figure 29.4 seem to differ from the results of a previous study by Tremblay and Schultz (1999). In their experiment, these authors delivered to monkeys one of three types of juice (A, B, and C, in decreasing order of preference) in fixed amounts. Trials were blocked, with one pair of juices employed in each block. Tremblay and Schultz found OFC neurons that responded to juice A but not to juice B during “A:B” blocks, and to juice B but not to juice C in “B:C” blocks. They interpreted these results to suggest that OFC neurons encode the “relative preference” of the juices.

Notably, the apparent discrepancy between the experimental results obtained in the two studies (Padoa-Schioppa and Assad, 2008; Tremblay and Schultz, 1999) leads to very different hypotheses regarding the nature of the encoding in OFC. On the one hand, the results of Tremblay and Schultz suggest that the OFC neurons encode the relative preference (i.e., the ordinal ranking) of the juices. On the other hand, the results of Padoa-Schioppa and Assad suggest that OFC neurons encode value in a cardinal (i.e., number-like) sense. From the point of view of economic theory, the issue of ordinal versus cardinal utility is foundational (Kreps, 1990).

How can the two sets of results be reconciled? One possibility is that recordings in the two studies examined different brain regions. Although the anatomical reconstructions in the two studies do not present clear differences, a precise distinction between different orbital areas requires refined histological procedures (Carmichael and Price, 1994) that were not conducted in either study. The difference between the behavioral paradigms used in the two studies suggests an alternative hypothesis. Specifically, it is possible that the observations of Tremblay and Schultz critically depended on the fact that trials were presented in blocks. In principle, a block design could affect neuronal responses in multiple ways. For example, in their study, “A:B” blocks could be considered high-value blocks, whereas “B:C” blocks could be considered low-value blocks. Their observations thus suggest that the activity of OFC neurons might adapt to the general behavioral context defined across many trials (the behavioral “condition”, as defined above). In this view, the changes in neuronal activity observed by Tremblay and Schultz were not due to menu dependence, but rather to a slowly adapting neuronal representation.

Taken together, the two sets of results thus suggest that neurons in OFC encode value in a cardinal sense (as opposed to ordinal preference), and that this neuronal representation of value adapts to the behavioral condition. Critically, whether the neuronal population examined by Padoa-Schioppa and Assad indeed undergoes such adaptation remains to be established.

Value Modulates Decision-related Signals in Parietal Cortex

In contrast with the OFC, parietal cortex appears to play an important role in linking sensory signals with motor commands, as well as guiding sensory attention, based on evidence from neurophysiological, neuroanatomical, and neuroimaging studies (Gnadt and Anderson, 1988; Colby et al., 1996). The importance of action for biological fitness implies that sensory-motor processing and attention should incorporate the value of alternative interpretations of sensory data for guiding behavior. By scaling neuronal activity that links...
sensation to action by value, motor systems may be biased to generate actions with greater behavioral utility. Similarly, scaling attention by the potential value of different stimuli may enhance the ability to detect and discriminate objects and events of high behavioral utility.

These ideas were first tested in a series of studies by Platt and Glimcher (1999) in which they explicitly probed the modulation of neuronal activity in the lateral intraparietal area (LIP) by the expected value of available options. Expected value \( E(x) \) is defined as the product of expected gain, \( x \), and the likelihood that gain will be realized (Arnaud and Nichole, 1982 (1662)). Prior studies had demonstrated that LIP neurons respond to visual stimulation as well as preceding gaze shifts to visible and remembered target locations (Gniadt and Andersen, 1988; Goldberg et al., 1990). Moreover, LIP neurons appear to signal the relative importance of visual stimuli for guiding subsequent behavior (Colby et al., 1996; Platt and Glimcher, 1997). Such observations suggested the hypothesis that LIP links sensation to action according to the expected value of each possible response.

Platt and Glimcher first tested this hypothesis in a task in which monkeys were not permitted to make choices, thus permitting the authors to vary the expected value of each option independently of potentially confounding factors associated with active decision-making. In this task, monkeys were cued by the color of a fixation stimulus to shift gaze to one of two peripheral visual targets, while the activity of single LIP neurons was monitored. The expected value of shifting gaze to each target was systematically varied by either delivering different amounts of fruit juice for correct gaze shifts to each of the targets, or by altering the probability that each of the possible gaze shifts would be cued across blocks of trials. In both cases, the authors found that when cue color, target location, and movement metrics were held constant, the activity of many neurons in area LIP was proportional to the expected value of a specific target. Similar correlations between neuronal activity and the expected value of a particular movement (either movement probability or expected reward magnitude) have been found in prefrontal cortex, the caudate nucleus and substantia nigra pars reticulata of the basal ganglia, and the superior colliculus (Salzman et al., 2005; Hikosaka et al., 2006). In a second study, Platt and Glimcher further demonstrated that, in the absence of an overt cue indicating which movement would be rewarded, the frequency with which monkeys chose each target was proportional to its expected value. Moreover, the activity of many LIP neurons paralleled these value-based decisions and was a direct function of target preference.

Taken together, these studies indicate that brain areas implicated in the conversion of sensory stimuli into action, such as LIP, incorporate the value of each available option. In these studies, however, the value of the available options remained constant throughout blocks of 50–100 trials, thus making it difficult to discern how closely LIP neurons track local fluctuations in value associated with the dynamics of ongoing decision-making. Sugrue, Corrado, and Newsome (Sugrue et al., 2004) extended these observations by probing decision-related activity in LIP using a virtual foraging task (Newsome et al., 2008). In their study, the likelihood of rewards associated with each of two targets fluctuated over time depending on the monkeys’ recent choices. Under these conditions, monkeys tended to match the rate of choosing each target to the relative rate of reinforcement of that target over both short and long timescales (matching behavior). Moreover, the responses of individual LIP neurons to a particular target corresponded to the history of relative payoffs associated with each target, with the greatest weight placed on the most recent trials. Similar results were found by Dorris and Glimcher (2004) in monkeys performing a frequency-dependent foraging task. In their study, LIP neurons were found to reflect a “value weight”: the activity of each neuron was modulated by the value of the corresponding visual stimulus divided by the value sum of all visual stimuli. Together, these and other studies suggest that behavioral decisions may be computed by scaling neuronal responses to sensory stimuli and motor plans by their expected value, thus modulating the likelihood of reaching the threshold for generating a particular percept or eliciting a specific action (Gold and Shadlen, 2001).

**Valuation Signals in Parietal Cortex are Independent of Modality**

Although concrete outcomes such as eating, drinking, or sex clearly motivate behavior, abstract goals such as information gathering or social interaction can also motivate behavior in the absence of hedonic experience and thus should contribute the value of any potential action. For group-living species such as humans and many non-human primates, the social environment strongly influences the behavioral context in which individuals pursue rewards, avoid punishments, evaluate risks, and make decisions. The adaptive significance of navigating a complex social environment suggests that social stimuli might evoke neural activity in some of the same circuits that process primary rewards and punishments, and
subsequently modulate the neural valuation functions that guide attention and action. For example, male primates use visual cues to predict female mating receptivity (Hrdy and Whitten, 1987) and field studies show that monkeys preferentially invest in relationships with dominant individuals (Cheney and Seyfarth, 1990). These observations suggest that the primate brain also computes valuation functions for specific social and reproductive stimuli that guide adaptive behavior.

These observations led Platt and colleagues to hypothesize a neural system linking social stimuli, such as images of faces or bodies, to the valuation functions guiding action. Deane and colleagues (2005) explored this hypothesis behaviorally using a “pay-per-view” task in which thirsty male rhesus macaques were given a choice between two visual targets. Orienting to one target yielded fruit juice; orienting to the other target yielded fruit juice and the picture of a familiar monkey. By systematically changing the juice amounts for each target as well as the picture shown, the authors estimated the value of different types of social and reproductive stimuli in a liquid currency. Their study revealed that male monkeys prefer a larger juice reward over a smaller juice reward or the opportunity to view female sexual signals of faces of high-ranking males, but require these large rewards to view the faces of low-ranking males and females (Figure 29.5a). Hayden and colleagues (2007) extended these findings by demonstrating that humans, like monkeys, will also pay more to view pictures of attractive members of the opposite sex than to view pictures of unattractive ones, even when the reward cues are implicit. Specifically, men placed a value of around half a cent (US) on the opportunity to view an attractive woman, whereas the value women placed on the opportunity to view an attractive man was not different from zero (Figure 29.5b).

These findings suggest that decisions based on value operate on a common currency that is independent of the modality of the goods under consideration or the actions they motivate. When monkeys choose between fluid and social rewards, they show consistent, apparently adaptive, preferences. Likewise, human subjects systematically trade off monetary and pictorial rewards. These observations provoke the hypothesis that the brain transforms information about disparate options into a common currency of value in which these options can be compared and evaluated. The studies described above suggest that the OFC encodes the abstract value of goods under consideration. These behavioral and neurobiological observations predict, then, that modulation of sensory-motor processing in cortical areas like LIP, which presumably lie downstream of abstract value processing in OFC, should be independent of the modality of the desired outcome. That is, it should not matter to an LIP neuron whether the option in its receptive field is rewarding because it is associated with juice, money, or the opportunity to look at an attractive member of the opposite sex – as long as revealed preferences indicate these goods have the same subjective value. Since the goal of action is presumably to maximize behavioral utility, sensory-motor decision processes should be modulated by value independent of the modality of the outcome.

Platt and colleagues tested this idea directly by examining the activity of LIP neurons in monkeys performing the pay-per-view task described above (Klein et al., 2008). In this study, the target associated with the display of an image was positioned within the receptive field of a neuron under study, whereas the other target was positioned in the other visual hemifield. Across blocks of trials, the identity of the class of images displayed for choosing the target in the receptive field was varied, and the volume of juice delivered for choosing either target was also varied. The authors found that LIP neurons were sensitive to both visual reward outcomes and juice reward outcomes associated with choosing the target in the neuronal receptive field (Figure 29.6a). Specifically, modulation of neuronal activity matched the value monkeys placed on seeing particular classes of images, in addition to the size of juice rewards; firing rates were highest when monkeys chose to view images of female reproductive areas, slightly lower when monkeys chose to view the faces of dominant males, and lowest when monkeys chose to view the...
faces of subordinate monkeys. Most importantly, LIP neurons encoded the contributions of expected visual outcomes and expected fluid outcomes to target value independently (Figure 29.6b). Thus, LIP neurons appear to signal the value of a visual target derived from the multiple potential outcomes, either visual or fluid, that could occur. Importantly, value modulation was not observed when monkeys were not permitted to choose where to look and were forced to make a particular behavioral response. This result is consistent with the idea that LIP neurons signal the relative value of the options available for orienting (Dorris and Glimcher, 2004; Sugrue et al., 2004) or the likelihood that they will look towards a particular target (Gold and Shadlen, 2001).

These observations indicate that value modulation of sensory-motor processing in parietal cortex, and presumably other areas that contribute to decision-making, is relative and not absolute, in contrast with value signals in OFC. Consistent with this notion, Platt and colleagues found that LIP neurons are also sensitive to the number of targets presented within their receptive fields (Klein et al., 2007). In that study, monkeys were simply rewarded for orienting to a single target opposite the receptive field of the neuron under study. While monkeys waited to make the required movement, an array of dots was illuminated within the receptive field. The firing rates of about half of the neurons studied were systematically suppressed as the receptive field. The firing rates of about half of the neurons studied were systematically suppressed as the receptive field. The firing rates of about half of the neurons studied were systematically suppressed as the receptive field. The firing rates of about half of the neurons studied were systematically suppressed as the receptive field. The firing rates of about half of the neurons studied were systematically suppressed as the receptive field. The firing rates of about half of the neurons studied were systematically suppressed as the receptive field. The firing rates of about half of the neurons studied were systematically suppressed as the receptive field. The firing rates of about half of the neurons studied were systematically suppressed as the receptive field. The firing rates of about half of the neurons studied were systematically suppressed as the receptive field.

These data suggest that LIP neuronal responses to stimuli and their associated actions may be normalized by the number of options available, similar to the process of divisive normalization characteristic of neurons in primary visual cortex (Heeger, 1993; Schwartz and Simoncelli, 2001). Since expected value depends on both the magnitude of expected reward and the likelihood that the reward will be delivered, normalization by the number of possible targets effectively rescales target valuation signals on a relative scale. Thus, neurons in parietal cortex, and most likely other areas that convert sensory information into action, appear to signal the relative value of choosing one of the available options for control of behavior.

**Valuation, Attention, and Decision-making**

Most studies of the representation of value by neurons in the primate brain have required monkeys to express their choices by orienting the eyes to a visual stimulus. Such studies have revealed that increasing the value of orienting to visual targets is associated with enhanced neuronal activity in a number of areas implicated in visual orienting behavior, including LIP (Platt and Glimcher, 1999; Coe et al., 2002; Sugrue et al., 2004), dorsolateral prefrontal cortex (Leon and Shadlen, 1999), the supplementary eye-fields (Amador et al., 2000), the caudate nucleus (Kawagoe et al., 1998; Watanabe et al., 2003), substantia nigra pars reticulate (Sato and Hikosaka, 2002), anterior (Ito et al., 2003) and posterior (McCoy et al., 2003) cingulate cortices, and the superior colliculus (Ikeda and Hikosaka, 2003). Value modulation in these areas has been interpreted to reflect decision-related computations that bias orienting to a particular target (Platt and Glimcher, 1999; Gold and Shadlen, 2001; Sugrue et al., 2004).

However, previous studies have also shown that neurons in most of these areas are sensitive to attention (Goldberg et al., 1990; Colby et al., 1996; Gottlieb et al., 1998), and lesions to many of these areas are often associated with deficits in attention. Since attention is typically controlled in animal studies by manipulating rewards, and rewarding events might also draw
In other words, attention and value are naturally linked and thus difficult to disentangle either behaviorally or neurophysiologically. In an initial attempt to address this issue, Bendiksby and Platt found that activation of LIP neurons was enhanced simply by increasing the value of all potential targets and that this enhancement was associated with predictable changes in behavioral response time (Bendiksby and Platt, 2006). In their study, monkeys performed a peripheral attention task in which they were rewarded for shifting gaze to a response target when one of two eccentric cues briefly flickered. The cues were presented sequentially, and flicker duration was titrated so that monkeys would perform correctly on about 70% of trials. The first cue to be illuminated was 80% likely to flicker, while the second was only 20% likely to flicker. Thus, monkeys should have paid closer attention to the first cue illuminated. Importantly, monkeys were uniformly rewarded with large or small squirts of juice in separate blocks of trials for correct performance—indeed, independent of which cue flickered. Under these conditions, monkeys responded more quickly when they could expect larger rewards than when they could expect smaller rewards, suggesting that action-encoding neural signals reached the threshold for movement initiation more rapidly when monkeys were more motivated (Figure 29.8a). At the same time, LIP neurons responded more strongly to visual cues in their receptive fields in large reward blocks than in small reward blocks, and these value-related modulations persisted until the time of the behavioral response (Figure 29.8b).

These results indicate that LIP neurons are sensitive to the value associated with visual stimuli, even when the stimulus is divorced from the ensuing behavioral response. Moreover, increasing stimulus value appears to increase both the gain of the initial neuronal response, as well as the sustained level of neuronal activity following stimulus presentation. A follow-up study by Bendiksby and Platt (2006) found similar results for LIP neurons in a visual orienting task in which attention was captured by a surprising visual stimulus and value was cued on each trial. Balan and Gottlieb have reported analogous gain modulation and baseline activity changes in LIP when task difficulty and attention, respectively, were manipulated (Balan and Gottlieb, 2006). Together, these observations suggest that attention and value jointly determine sensory-motor processing in LIP and possibly other areas that connect sensation and action. More research is needed to determine precisely how value and attention influence information processing by neurons in different brain areas during decision-making.

### EVALUATION OF EVENTS AND ACTIONS IN POSTERIOR CINGULATE CORTEX

#### Anatomical, Clinical, and Neuroimaging

**Significance of Posterior Cingulate Cortex**

Evidence reviewed in this chapter suggests that the abstract value of goods under consideration for choice is represented in the OFC. Translation of abstract valuation signals represented in OFC, and possibly elsewhere, into action appears to involve value-related modulation of cortical and sub-cortical areas involved in sensory-motor integration. One important question is how the abstract value signals in OFC, and other areas, are evaluated and bound to events and actions in order to adaptively influence future behavior.

Based on the anatomy, one potential candidate is the posterior cingulate cortex (CGp). Posterior cingulate cortex is strongly interconnected with brain areas known to be involved in learning and motivation or that are sensitive to reinforcement contingencies, including the anterior and lateral thalamic nuclei (Gabriel et al., 1991), the caudate nucleus (Powell, 1978; Yeterian and Van Hoesen, 1978; Baleydier and Mauguere, 1980), and medial portions of the OFC.
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FIGURE 29.8  Increasing target value reduces reaction time and increases the gain of visual responses in LIP. Monkeys performed a peripheral attention task and earned large and small juice rewards for correct performance in different blocks of trials. (a) Reaction times for two monkeys as a function of reward size; (b) PSTH for a single LIP neuron plotting firing rate as a function of time, aligned on onset of the visual cue in the response field (left), discriminative event (middle), or gaze shift away from the response field (right). Both the gain of the visual response, and sustained activity, increased with increasing target value, independent of the movement away from the response field.

(Baleydier and Mauguiere, 1980). In addition, CGp is strongly interconnected with anterior cingulate cortex, which contains neurons carrying nociceptive (Sikes and Vogt, 1992) and reward-related information (Niki and Watanabe, 1979; Shidara and Richmond, 2002; Ito et al., 2003) and which is capable of activating brain reinforcement circuits when artificially activated (Goodall and Carey, 1975; Spence et al., 1985). CGp is also particularly well-situated anatomically to receive information about visual events, action, and attention, including strong connections with parietal cortex (Baleydier and Mauguiere, 1980; Pandya et al., 1981; Vogt and Pandya, 1987; Cavada and Golman-Rakic, 1989a, 1989b; Andersen et al., 1990; Blatt et al., 1990; Morecraft et al., 1993), dorsolateral prefrontal cortex (Barbas and Mesulam, 1985; Selemon and Goldman-Rakic, 1988; Barbas and Pandya, 1989), and the frontal eye-fields (Barbas and Mesulam, 1981; Vogt and Pandya, 1987). CGp thus receives appropriate inputs to signal the motivational significance of visual events and action.

Consistent with its anatomical connections, clinical evidence suggests that posterior cingulate cortex contributes to visual orienting and navigation, attention, emotion, and learning and memory (Maddock, 1999). The first manifestations of Alzheimer’s disease, learning and memory impairment, have been linked to a less than 20% decrease in the metabolic activity of posterior cingulate cortex (Minoshima et al., 1997). Damage to CGp is also associated with spatial disorientation and navigational impairments (Cammalleri et al., 1996; Takahashi et al., 1997; Katayama et al., 1999). Posterior cortical atrophy (or PCA), which is association with depression of CGp metabolic activity, is characterized by optic ataxia and disturbances of visual attention (Hof et al., 1993, 1997; Fletcher, 1994; Braak et al., 1996). Conversely, elevated activity in posterior cingulate cortex is found in a variety of personality, mood, and anxiety disorders, including schizophrenia, major depression, obsessive-compulsive disorder, and social phobia (Maddock, 1999), all of which can be viewed to some degree as disorders of behavioral valuation.

Additionally, neuroimaging studies demonstrate that posterior cingulate cortex is activated by changes...
in subjective motivational state, as well as by attention to events and actions. For example, Small and colleagues (2001) tested human subjects before and after feeding them with chocolate to satiation. Intriguingly, BOLD signal in CGp was elevated when subjects rated chocolate as either highly pleasant or highly unpleasant, rather than neutral. Maddock and colleagues (2003) also demonstrated activation of CGp by presentation of both positive and negative emotion-laden words, as well as retrieval of words presented in negative emotional contexts (Maratos et al., 2001).

Activation in CGp has also been linked to errors in reward prediction during risky decision-making (Dickhaut et al., 2003). More recently, Kable and Glimcher (2007) demonstrated that CGp activation varies systematically with time-discounted value in an inter-temporal choice task. Functional imaging studies have also revealed CGp activation following illumination of visual stimuli (Yamasaki et al., 2002) following a shift in visual attention (Kim et al., 1999; Hopfinger et al., 2000, 2001; Mesulam et al., 2001; Small et al., 2003), during overt visual orienting (Berman et al., 1999), and during visuospatial navigation (Flitman et al., 1997; Ghaem et al., 1997; Pine et al., 2002). Moreover, the BOLD signal in CGp correlates with improvements in visual detection performance associated with valid spatial cues in peripheral attention tasks in humans (Small et al., 2003). Together, these observations suggest a role for CGp in signaling motivationally significant events and actions, as well as perhaps their subjective value for guiding future behavior.

Neurophysiological Evidence that CGP Plays a Role in Evaluating Behavioral Events

Neurophysiological studies conducted in animals support the idea that posterior cingulate cortex contributes to the evaluation of stimuli as well as behavioral actions. For example, CGp neurons respond to visual stimulation (Kalra and Whitteridge, 1973; Olson and Musil, 1992; Olson et al., 1996) and their responses depend on behavioral context (Dean et al., 2004a).

Specifically, CGp neurons respond most strongly to visual events that are unpredictable in space or time, and the strength of these neuronal responses predicts how accurately monkeys subsequently orient (Dean et al., 2004). CGp neurons respond strongly after orienting movements, and these responses are anchored to locations in space rather than to the locus of retinal stimulation (Dean et al., 2004a; Dean and Platt, 2006). CGp neurons also respond following the delivery of unpredictable rewards as well as following the omission of predictable rewards (McCoy et al., 2003).

Moreover, the CGp responses to task-related events are modulated by their associated value (McCoy et al., 2003). Thus, CGp neurons appear to report potentially significant events in a manner divorced from pure sensory properties or the actions these events might guide. CGp thus carries information that could in principle be used to link events and outcomes in a context-dependent fashion. Such information might inform sensory-motor processing in brain areas, such as LIP, that contribute to action selection (McCoy et al., 2003; Dean et al., 2004b).

Evaluative Signals in CGp are Subjective

It is well known that choosers demonstrate idiosyncratic attraction or aversion to options associated with risky payoffs. Thus, risk sensitivity provides a powerful assay to dissociate subjective representation of value or utility from the representation of objective rewards. Recent neuroimaging studies in humans have revealed that preference for a risky option is associated with increases in neuronal activity in the ventral striatum and posterior parietal cortex (Kuhnen and Knutson, 2005; Huettel et al., 2006; Preuschoff et al., 2006). Moreover, choosing a risky option activates the dorsal striatum, posterior cingulate cortex, and precuneus (Dickhaut et al., 2003) as well as amygdala (Hsu et al., 2005) and insula (Huettel et al., 2006).

These observations suggest that the neural mechanisms that bind value to events and action must also be sensitive to risk if these processes contribute to choice. To test this idea, McCoy and Platt (2005) used a visual gambling task to assess whether previously-reported contextual modulation of neuronal activity in CGp reflects subjective value or the objective properties of available rewards. Monkeys were given a choice between two options on a computer monitor. Choosing the safe option always resulted in a medium-sized squirt of juice. Choosing the risky option resulted in a 50% chance of a large squirt of juice and a 50% chance of a small squirt of juice. Surprisingly, monkeys strongly preferred the risky option when both had the same expected value (Figure 29.9a). In fact, monkeys continued to choose the risky option even when the probability of a larger than average reward was only 1/3. CGp neurons closely mirrored this behavioral bias, rather than representing the objective value of each target (Figure 29.9b). Further, CGp neuronal activity was correlated with subjective target value estimated from the history of monkeys’ choices and rewards received (McCoy and Platt, 2005). These data are consistent with the hypothesis that CGp contributes to decision-making.
by evaluating external events and actions with respect to the subjective preferences of the animal. One concern might be whether this modulation of neuronal activity in CGp associated with choosing risky options reflects arousal. However, heart rate (a somatic correlate of physiological arousal) did not vary between high-risk and low-risk blocks of trials.

Risk-seeking by monkeys violates expectations based on the assumption of diminishing marginal utility of rewards. One possible explanation for monkeys’ preferences could be that monkeys focus on the large reward and ignore bad outcomes. Hayden and Platt tested this hypothesis by examining the relationship between risk preference and delay between trials (Hayden et al., 2007). They found that monkeys’ preference for risk declines with increasing delays and reverses when delays increase beyond 45 seconds. These results can be explained by “string theory” (Rachlin, 2000), which proposes that the salience of the large reward, and the expected delay until that reward can be obtained, influence valuation of a risky option. In this model, the value of the risky option is only updated following salient payoffs (in this case, the large rewards) and all rewards are discounted by the delay since the last reward. When the time between trials is short the value of the large reward delivered for choosing the risky option remains essentially unmitigated by the delay, but when the time between trials is long the large reward is heavily discounted. This model accurately predicts the systematic preference reversal of monkeys in this task. Similar processes have been proposed to operate in humans who pursue the immediate, intense “high” of certain drugs of abuse, while simultaneously discounting the delayed, longer-term “low” of withdrawal (Bickel et al., 1999; Bernheim and Rangel, 2004). Alternatively, monkeys may have a concave utility function for reward when the time between trials is short, but the utility function becomes convex when the time between trials is long. In principle, these possibilities might be distinguished using neurophysiological data.

### Attention, Learning, and the Posterior Cingulate Cortex

The observation that some CGp neurons respond equivalently to the delivery of larger than average rewards and to the omission of predicted rewards is consistent with a role for this area in highlighting motivationally significant events for the evaluation and control of action (McCoy et al., 2003). The correspondence of neuronal activity in CGp with subjective risk preferences may also reflect subjective focus on the highly salient jackpots occasionally delivered for choosing the risky option (Hayden and Platt, 2007). In addition to guiding future action selection, neuronal activity in CGp may also play a role in learning. Reward modulation of neuronal activity in CGp is consistent with attentional theories of learning, which posit that reward prediction errors highlight motivationally significant events (Pearce and Hall, 1980). According to this idea, neuronal activity correlates with the extent to which outcomes differ from expectations, either positive or negative. While such a signal would not carry information about what needs
to be learned, such a signal would instruct when and how effectively learning should occur. Some of the value-related modulations in CGp may thus contribute to attention for learning. Consistent with this idea, lesions of posterior cingulate cortex in rabbits impair certain forms of associative conditioning, and neuronal activity in this same area changes systematically during learning (Gabriel, 1990). However, the homology of posterior cingulate cortex in rabbits to CGp in primates remains uncertain, and thus this hypothesis awaits further study.

### NEURO-COGNITIVE MODELS OF CHOICE

As described in previous sections, neuronal correlates of value exist in the OFC, CGp, and LIP. In addition, other studies suggest that value might also be encoded by neurons in numerous other brain regions, including dorsolateral prefrontal cortex (Lee and Wang, 2008), premotor cortex (Roesch and Olson, 2003), frontal eye-fields (Roesch and Olson, 2003), supplementary eye-fields (Stuphorn et al., 2000; Roesch and Olson, 2003), superior colliculus (Ikeda and Hikosaka, 2003), basal ganglia (Kawagoe et al., 1998; Doya and Kimura, 2008), amygdale (Paton et al., 2006), and centromedian nucleus of the thalamus (Minamimoto et al., 2005). Although redundancy is hardly an exception in the nervous system – for example, in the primate brain, arm movements are represented in some six to eight different areas, and eye movements are represented in at least six different areas – it is reasonable to ask why there are so many representations of value in the primate brain. Here we propose that value signals expressed by different neuronal populations contribute to different mental processes. In sensory areas, value signals may contribute to perceptual attention (a process of choice between different sensory stimuli); in frontal areas, value signals may contribute to economic choice (a choice between different goods); in motor areas, value signals may contribute to action selection (a choice between different motor acts). To discuss this proposal, we shall specifically discuss value representations in OFC and LIP, because neuronal value signals in these areas have been studied in the greatest detail.

### Value Modulations in the Sensory, Goods, and Motor Domains

The rationale of our proposal rests on the observation that value representations in different brain areas are not identical. As described in previous sections, neurons in OFC represent the value of goods per se, independently of how goods are visually presented to the monkey, and independently of the action with which the monkey reveals its choice (Figure 29.2d). In contrast, neurons in LIP represent value as a modulation of responses encoding the spatial location of the visual stimulus or the eye movement necessary to express the choice. Another important difference is that the value representation in OFC is menu invariant, whereas the value representation in LIP is menu dependent.

In sensory areas, value modulations may be largely coextensive with the allocation of attention. For example, a rich literature shows that attention modulates visual responses in LIP, and this area can be thought of as representing a map of salient locations in the visual field (Goldberg et al., 2002). From a psychological point of view, in most experimental paradigms attention and value are naturally linked (Maunsell, 2004). On the one hand, attention is typically drawn to a particular visual stimulus by selectively increasing the value associated with that stimulus. On the other hand, any manipulation of the value associated with a particular visual stimulus inevitably influences the attention allocated to that stimulus. Thus, attention and value are often confounded (Maunsell, 2004). Several observations are relevant for evaluating the contributions of attention and value to neuronal activity in LIP. First, Bendiksby and Platt demonstrated that both attention and value contribute independently to neuronal activity in LIP when these two factors are dissociated behaviorally. In their study, value and attention modulations jointly determined changes in behavioral performance typically associated with attention, and were independent of the movement made by the animal (Bendiksby and Platt, 2006). Second, value modulations in LIP take the form of a value weight: the response to one particular stimulus is modulated by the ratio of the value of that stimulus to the value sum of all other visual stimuli (Doris and Glimcher, 2004) In other words, the “total value modulation” (i.e., the value modulation integrated over all spatial locations) is a constant and does not change over time. What does change over time, from one moment to the next, is how the total value modulation is distributed across spatial locations. This observation is consistent with an attentional modulation. Indeed, attention is generally conceptualized as a scarce resource that can be competitively allocated to different stimuli or spatial locations (Bundesen, 1990; Desimone and Duncan, 1995), an idea consistent with value modulating perceptual processing and orienting behavior. (Bundesen, 1990, in fact defines attention as a choice process taking place through value weights.)
In conclusion, value signals in sensory areas might underlie perceptual attention.

In motor areas, value signals could contribute to action selection. From a computational point of view, planning and controlling even a simple voluntary motor act (such as an arm reaching movement) is very challenging. It involves resolving multiple problems with infinite solutions and many degrees of freedom (Muss-Ivaldi and Bizzi, 2000; Wolpert and Ghahramani, 2000). One reasonable hypothesis is that the nervous system might partly solve this problem through mechanisms in which different motor plans compete with one another. For example, in the model of Glimcher and colleagues, a value is associated with each motor plan, and a single motor act eventually emerges through a winner-takes-all process (Glimcher et al., 2005). Behavioral results in humans and other species support this view (see Chapter 8 of this volume) Value modulations that exist in genuinely motor areas (Stuphorn et al., 2000; Ikeda and Hikosaka, 2003; Roesch and Olson, 2003; Chapter 26 of this volume) might thus contribute to action selection.

In areas that encode the value of goods per se, such as OFC, value signals could underlie economic choice. Consider again a person sitting in a restaurant and choosing between tuna tartare and fried calamari. Presumably, the person assigns a value to the tuna and a value to the calamari, and then compares the two values to make a decision. OFC neurons encoding the offer value seem to capture this valuation process, because different neurons encode the value of different available goods. The actual decision might then emerge through a winner-takes-all mechanism, similar to the one thought to mediate action selection.

“Goods-based” and “Actions-based” Models of Economic Choice

The proposal that value signals that are independent of the sensory-motor contingencies of choice (as in OFC) contribute to the choice between goods does not necessarily imply that economic choices completely unfold within these neuronal representations of value. With respect to this fundamental issue, two alternative hypotheses can be considered: the “goods-based” model and the “actions-based” model.

According to the goods-based model, economic choice is an independent cognitive module (Fodor, 1983; Pinker, 1997) – a set of mental and neuronal processes that take place in a space where goods are represented as such. This proposal thus assumes a level of mental abstraction – the space of goods – computationally removed from sensory and motor representations. Values are assigned online to the available goods, based on their properties and on the internal state of the animal at the time of choice. Formally, the value assigned to a given good is described as a function \( V(a_1, a_2, \ldots) \) of multiple arguments \( a_1, a_2, \ldots \) that describe the good, the motivational state of the animal, the choice contingencies (probabilities, costs, delays, etc.), and the behavioral context of choice. The rules and mechanisms that underlie the computation of the neuronal value function are currently unknown, although neuronal responses recorded in OFC demonstrate that this abstract value function is computed. The key feature of the goods-based model is that economic choice fully takes place in the space of goods. In other words, when an individual chooses between goods X and Y, values are assigned to the two goods and a decision is made between these values. Once one good is chosen, the individual plans and executes a suitable motor action to implement the choice. According to the good-based model, however, action selection is a process distinguished from and following economic choice. In this sense, the good-based model of economic choice is modular and sequential.

In contrast, according to the actions-based model, economic choices are embedded in premotor processes of action selection. Several models of decision-making can be viewed as variations on the actions-based model (see Chapters 26 and 31 of this volume; Dickinson and Balleine, 2002; Glimcher et al., 2005). In one version of the model, originally proposed by Skinner (1953), the behavior of the animal is described simply in terms of sensory stimuli and motor responses, and the problem of choice is essentially reduced to a problem of associative learning. During training, the animal learns the association between a set of stimuli and the rewarded motor response; the animal thus develops a look-up table to be consulted in future choices. In a more recent version of the action-based model, proposed by Glimcher and colleagues (2005), values are learned through experience (possibly in an abstract representation) through mechanisms of reinforcement learning (Sutton and Barto, 1998). At the time of choice, values are retrieved and funneled through the action-selection system, such that a value is attached to each possible course of action. Economic choice thus unfolds as a process of action selection, through a winner-takes-all mechanism. In this view, brain areas and neuronal populations responsible for action selection (such as LIP) represent a common pathway for different types of decision-making; they are the substrate upon which choices are actually generated (Glimcher et al., 2005). Hence, according to the actions-based model,
Comparing Goods-based and Actions-based Models

A priori, the goods-based and the actions-based models of choice are both legitimate proposals, and we shall now discuss some of their merits. The actions-based model has traditionally been more prominent. Two lines of reasoning have been presented to support this model. First, because it builds more or less directly on theories of reinforcement learning, the actions-based model is often presented as one aspect of a more general psychological model of behavior. In principle, a unitary model might seem more parsimonious and thus desirable. At the same time, it can be noted that learning and choice are conceptually distinct and dissociable mental processes. For example, there can be choice in the absence of measurable learning (as in the experiments of Padoa-Schioppa and Assad), as there can be learning in the absence of choice (as in classical and instrumental conditioning). Hence, one particular model of learning does not imply one particular mechanism supporting economic choice. Another argument often presented to support actions-based models is that, at the neuronal level, value signals were first observed in brain areas involved in sensory-motor processes (Kawagoe et al., 1998; Platt and Glimcher, 1999; Ikeda and Hikosaka, 2003; Roesch and Olson, 2003; Chapter 26 of this volume). However, this is not an argument against the goods-based model, because value signals in sensory-motor areas could underlie action selection but at the same time make no contribution to economic choice.

Two arguments have been presented to support the goods-based model (Padoa-Schioppa and Assad, 2008). First, the goods-based model seems in principle more efficient because it is modular (Simon, 1962; Pinker, 1997). Planning and controlling movements is computationally challenging. In a modular architecture, the nervous system would break down the complex operation [choosing and moving] into two separate and simpler operations, [choosing] and [moving]. If convolving the control of any motor act with economic choice (actions-based model) requires extra computational power, however minimal, the great redundancy of the motor systems would make a non-modular design enormously more expensive than a modular design. Importantly, natural selection does not always find optimal solutions. It is possible that primates may have evolved to make actions-based economic choices, even though this process may be less efficient than making goods-based choices. In this sense, the OFC results reviewed above can be viewed as an existence proof. Indeed, neurons in OFC encoding the value of offered and chosen goods encode the variables necessary for efficient, goods-based economic choices. One weakness of this argument, however, is that while OFC provides an abstract representation of value, there is no evidence yet demonstrating that the entire choice process (including value comparisons) fully takes places in the abstract representation of goods. The key tenet of the goods-based model thus remains to be tested.

The other argument presented to favor the goods-based model as opposed to the actions-based models builds on observations in neuropsychology. Actions-based models of choice instantiated in specific sensory-motor areas, such as LIF (Glimcher et al., 2005) or the basal ganglia (see Chapter 26), often overlook the fact that lesions to these areas do not typically influence economic choice behavior per se. For example, lesions of the parietal cortex result in visuo-spatial deficits such as hemi-neglect and Balint’s syndrome (Colby and Olson, 1999). In contrast, economic choices are typically disrupted by OFC lesions (Bechara et al., 1996; Pasquier and Petit, 1997; Rahman et al., 1999; Fellows and Farah, 2007; Koenigs and Tanel, 2007). In other words, unlike OFC, sensory-motor areas are not strictly necessary for making economic choices, although they are required for implementing them. Notably, while this line of reasoning argues against specific versions of the actions-based model, it does not prove (or explicitly argue for) the goods-based model.

Two important points should be emphasized. First, the goods-based model only applies to choices between goods (economic choices). However, during the normal course of behavior, different valuation processes occur simultaneously as animals make choices in the sensory, goods, and motor domains. Second, behavior often evolves from choice to habit, thus requiring less deliberation – a process mirrored by changes in neuronal circuitry (Graybiel, 2005).

How can the two models be tested more directly? Both models conceptualize economic choice as a two-stage mental process where values are initially assigned to the available goods and a decision (i.e., a comparison between values) is subsequently made (Glimcher et al., 2005; Padoa-Schioppa et al., 2006). Apart from the role of learning, the two models differ on one critical point: according to the goods-based model, choice should be completely processed within an abstract representation of goods. Because an abstract representation of value exists in the OFC,
distinguishing between the two models requires establishing whether the decision process that follows valuation (that is, the winner-takes-all mechanisms through which different values are compared) takes place in the space of goods or in the space of actions. In principle, this question can be addressed by separating in time the choice between goods and the selection of action. This issue thus remains an important question for future work.

CONCLUSION

Multiple representations of value exist in the primate brain. Specifically, neurons in the orbitofrontal cortex encode the value subjects assign to different goods, independently of how the goods are presented or the action necessary to implement choice. Moreover, the representation of value in the OFC is menu invariant – neuronal responses encoding the value of one particular good do not depend on what other goods are available at the same time. In contrast, neurons in parietal cortex are sensitive to the value of a particular location in space or a particular action. Whereas representations of value in OFC are “absolute,” value signals in parietal cortex are “relative” – each neuron is modulated by the ratio of the value of the corresponding location/action to the value sum of all locations/actions. Finally, neurons in posterior cingulate cortex appear to encode an ongoing estimate of the subjective value or salience of extra-personal events and actions; these signals may update value-related information in brains areas like the parietal cortex.

These observations suggest that different neuronal representations of value in different parts of the brain contribute to distinct computational processes. In sensory areas, value-related modulation in neuronal activity might promote selective processing of high-value stimuli by attention. In frontal cortex, neurons representing abstract value could contribute directly to the selection of one among multiple available goods based on subjective preference. Finally, in sensory-motor areas, value modulations might promote the selection of one particular action among many to achieve a behavioral goal.

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