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# Neuronal Representations of Value

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## INTRODUCTION

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### Value and Decision-making in Evolutionary Perspective

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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.

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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.

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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.

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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

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

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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.

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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.*, 1996; Rahman *et al.*, 1999), 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).

p0080 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.

p0090 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

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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.

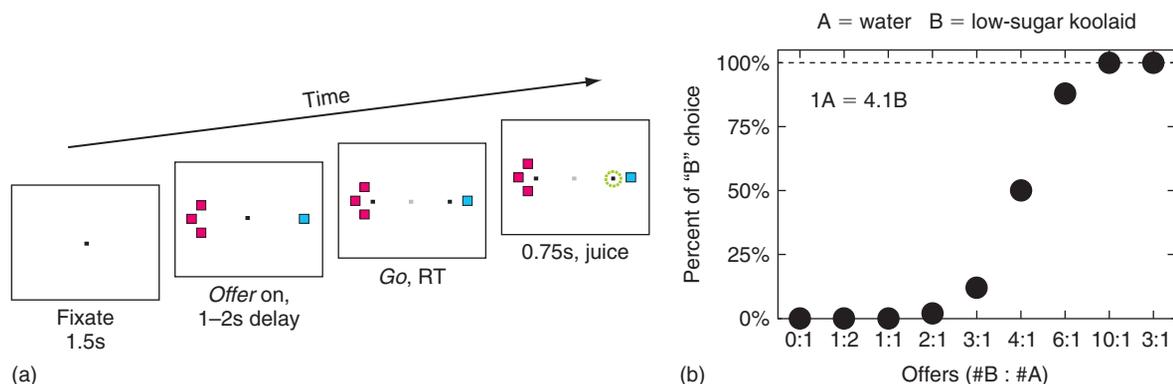
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In a recent study, Padoa-Schioppa and Assad used this behavioral paradigm to examine the activity of neurons in OFC as a function of subjective value (Padoa-Schioppa and Assad, 2006). Figure 29.2 illustrates the activity of one representative cell. 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 higher when the monkey chose 2A and when it chose 6B (*chosen value* = 6); the neuronal activity was highest when the monkey chose 3A and when it chose 10B (*chosen value*  $\approx$  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).

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A further analysis confirms that U-shaped responses like these encode the subjective value monkeys assign

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f0010 **FIGURE 29.1** An economic choice task. (a) At the beginning of each trial, the monkey fixated the center of the monitor. Two sets of squares appeared on opposite sides of the fixation point (offer). Different colors of the squares indicated different juice types and the number of squares indicated the juice amount. After a randomly variable delay (1–2s), two saccade targets appeared near the offers (“Go”). The monkey indicated its choice and maintained fixation on the saccade target for 0.75s before juice delivery (juice). The trial was aborted if the monkey broke fixation before the Go. For any juice pair, the quantities of the two juices varied randomly. Trials with the three juice pairs were randomly interleaved and, for any given pair of offers (offer type), left/right positions were counterbalanced. (b) Choice pattern. In this session, the monkey chose between water (juice A) and low-sugar Kool-Aid (juice B). The plot shows the percentage of trials in which the monkeys chose juice B (y-axis) for various offer types (x-axis). A sigmoid fit provides the measure of the relative value  $1A = 4.1B$ . Adapted from Padoa-Schioppa and Assad (2006, 2008).

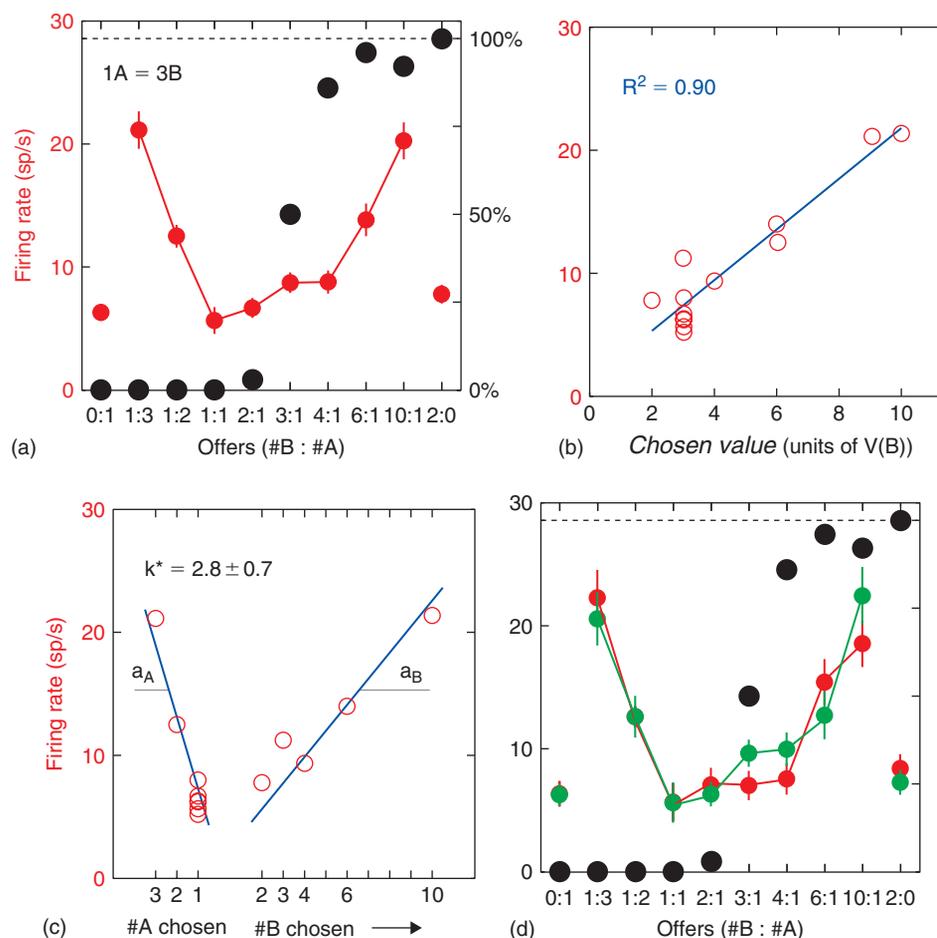
p0130 to the juice, as opposed to any physical property of the juices. In Figure 29.2c, the activity of the same neuron is plotted as a linear function of the number of units of A (#A) and number of B (#B) chosen. The hypothesis that neuronal activity encodes the *chosen value* leads to a simple prediction 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  $k^* = 2.8(\pm 0.7)$  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  $k^* = -0.13(\pm 0.15) + 1.05(\pm 0.15)n^*$  (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



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**FIGURE 29.2** Example OFC neuron encoding the *chosen value*. (a) Black symbols represent the behavioral choice pattern and red symbols represent the neuronal activity ( $\pm$ s.e.m.). We conventionally express values in units of  $V(B)$ . The cell activity is low when the monkey chooses 1A and when it chose 3B (offer types 1B:1A, 2B:1A, 3B:1A; *chosen value* = 3); it is higher when the monkey chooses 2A and when it chose 6B (offer types 1B:2A, 6B:1A; *chosen value* = 6); and it is highest when the monkey chooses 3A and when it chose 10B (offer types 1B:3A, 10B:1A; *chosen value*  $\approx$  10). (b) Same neuronal responses plotted against the variable *chosen value* (expressed in units of  $V(B)$ ). A linear regression provides  $R^2 = 0.90$ . (c) Same neuronal response plotted against the number of A and B chosen (linear scale). The slope ratio  $k^*$  provides a neuronal measure of relative value statistically indistinguishable from the behavioral measure. (d) Here, the cell activity 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 neuronal responses recorded for the two sets of trials are essentially identical, indicating that the activity of this neuron was independent of the visuomotor contingencies of choice. This was consistently true for over 95% of neurons in OFC. Adapted from Padoa-Schioppa and Assad (2008).

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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

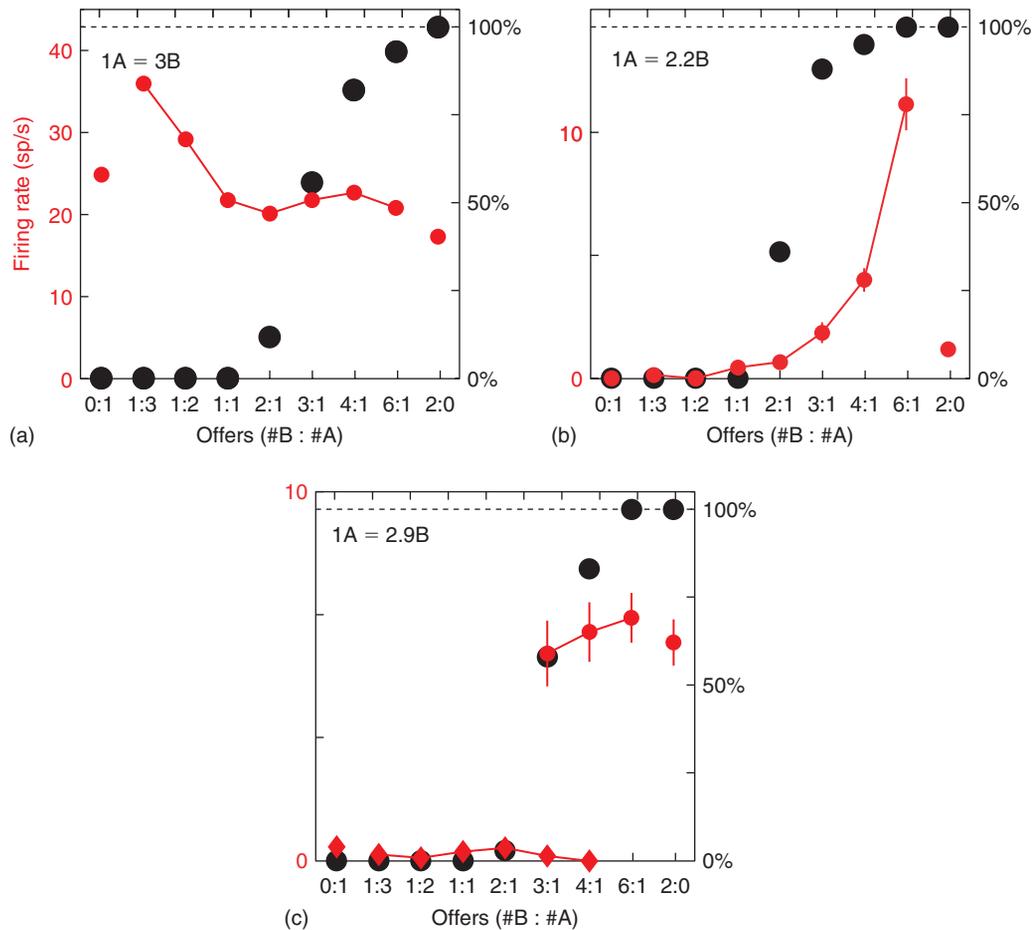
of value removed from sensory and motor contingencies emerged subsequent to the divergence of primates and rodents from a common ancestor (Roesch *et al.*, 2006).

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

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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

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f0030 **FIGURE 29.3** Different types of neuronal response patterns in OFC. Activity of three neurons encoding the variables (a) offer value A, (b) offer value B, and (c) taste. All conventions are as in Figure 29.2. Adapted from Padoa-Schioppa and Assad (2006) and Padoa-Schioppa (2007).

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.

p0170 In a second study, Padoa-Schioppa and Assad (2008) examined specifically whether the representation of value in OFC depends on the menu – that is,

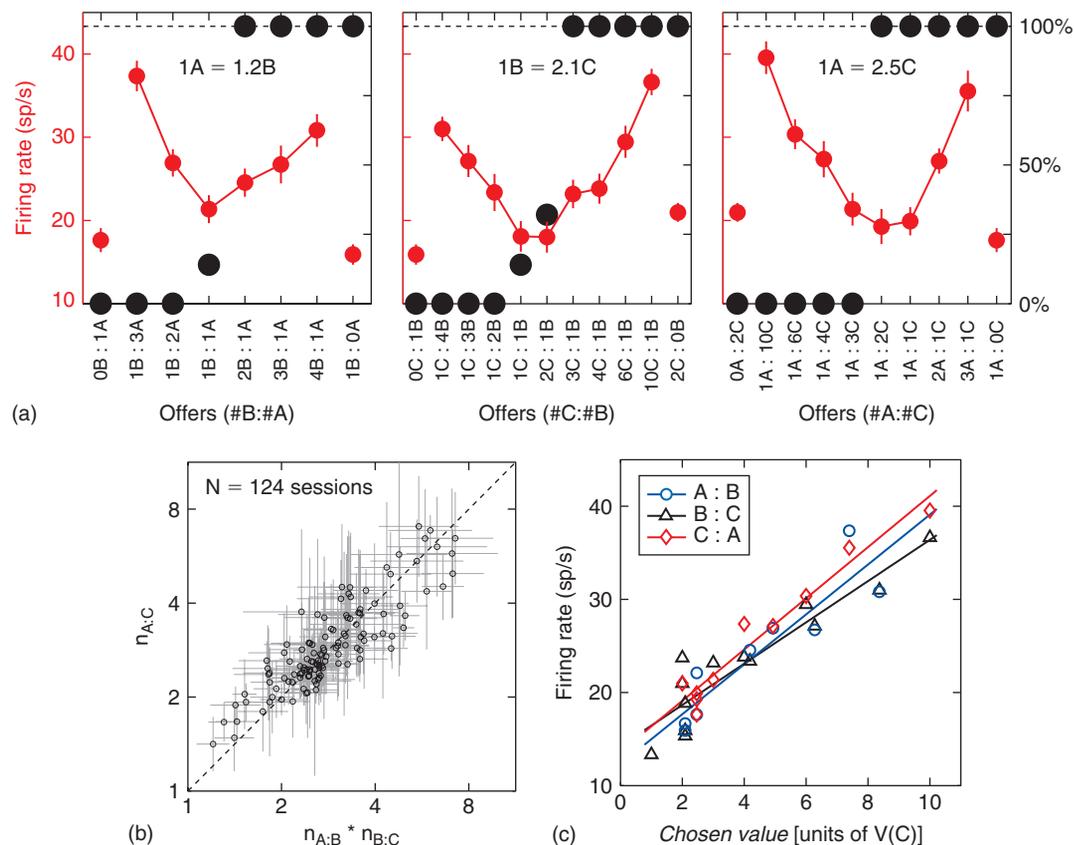
### BOX 29.1

#### TRANSITIVITY

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  $n_{A:B} = n_{B:C} \cdot n_{A:C}$  (*value transitivity*) (Padoa-Schioppa and Assad, 2008).

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**FIGURE 29.4** Menu invariance in OFC. (a) Responses of one neuron encoding the *chosen value*. The three panels refer to trials A:B, B:C, and C:A. In each panel, black symbols represent the behavioral choice pattern and red symbols represent the neuronal activity ( $\pm$ s.e.m.). Relative values (top left) combine according to transitivity (because  $1.2 * 2.1 \approx 2.5$ ). The neuronal response encodes the *chosen value* independently of the juice pair. (b) 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  $n_{A:C} = n_{A:B} * n_{B:C}$ . 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 variable chosen value, and different symbols and colors refer to the three juice pairs (blue circles for A:B, black triangles for B:C, and red diamonds for C:A). Each symbol represents one trial type. The regression lines are obtained from a full-model analysis of covariance (ANCOVA). Adapted from 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 fits combine according to value transitivity, in the sense that  $1.4 * 1.9 \approx 2.6$ . 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 *chosen value* independently of the juice pair. This can be observed most clearly in Figure 29.4c, where the same neuronal response (y-axis) is plotted against the variable *chosen value* (x-axis) and the three colors represent the three juice pairs. The three regression lines (from an analysis of covariance) are statistically indistinguishable from one another, indicating that the activity of the cell encodes the *chosen value* independently of the menu. Similarly, the activity of neurons encoding the *offer value* or the taste of one particular juice did not

typically depend on the other type of juice offered in the same trial. Across a population of 868 neuronal responses, 767 (88%) were invariant for changes of menu (a “neuronal response” is defined as the activity of one neuron in one time window).

p0190 Whether the activity of neurons in OFC is causally related to economic choice remains an open question. Nonetheless, it is worth noting that neurons in OFC encoding economic value independently of other options available could in principle provide a neuronal explanation for preference transitivity. Indeed, in most typical situations, human and animal economic choices satisfy preference transitivity (Mazur and Coe, 1987). When transitivity violations are observed (Tversky, 1969; Navarick and Fantino, 1972; Shafir, 1994), it is generally because assigned values depend on the menu (Grace, 1993; Shafir, 1994). In other words, menu-invariant values imply preference transitivity. If assigned values (as measured at the behavioral level) result from the activity of neurons in the OFC, then menu-invariant responses in OFC imply menu-invariant values, which in turn imply transitive preferences. As described below, menu invariance may be a trait specific to OFC. Indeed, in other brain areas where this issue has been examined, signals reflecting the value of one particular option are modulated by the value of other options available at the same time.

### s0070 Ordinality, Cardinality and Neuronal Adaptation

p0200 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.

p0210 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.

## VALUATION SIGNALS IN PARIETAL CORTEX

### 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 neurological, neurophysiological, 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.

p0250 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 intra-parietal 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 (Gnadt 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.

p0260 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 p0270 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

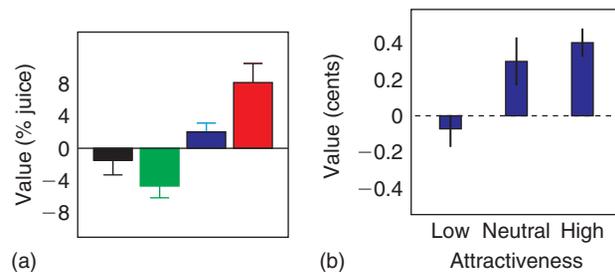
s0100

Although concrete outcomes such as eating, drinking, or sex clearly motivate behavior, abstract goals p0280 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.

p0290 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. Deaner 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 forego larger juice rewards in order to view female sexual signals or 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).

p0300 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



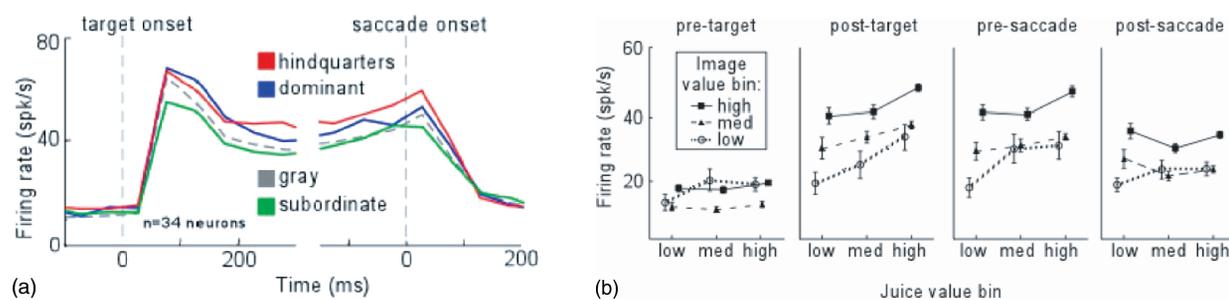
**FIGURE 29.5** Monkeys and people value visual social information. (a) Average value (in percent juice volume) of the opportunity to view an image of a gray square (gray), subordinate male face (green), dominant male face (blue), or female perineum (red), for five male macaques. Value was estimated using a “pay-per-view” task in which monkeys chose between fluid rewards and fluid rewards paired with images. (b) Average value (in cents) of viewing the face of a female of low, neutral, or high physical attractiveness, for 20 male subjects. Value was estimated using a “pay-per-view” task in which people chose between monetary rewards and monetary rewards paired with images.

f0050

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

p0310



**FIGURE 29.6** LIP neurons encode the abstract value of orienting to a visual stimulus. (a) Peri-stimulus time histogram (PSTH) plotting firing rate of a population of neurons as a function of time, aligned on either target onset or the saccade monkeys used to report their preference. On each trial, the monkeys chose to view an image associated with a target in the response field of the neuron under study. Images were female perinea (red), dominant male faces (blue), subordinate male faces (green), or gray squares (gray). (b) LIP neurons encode both fluid value and juice value. Firing rate is plotted in four consecutive 200-ms bins, and sorted by juice value and image value. ANOVA for juice value and image value were significant, but there was no interaction between these variables.

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).

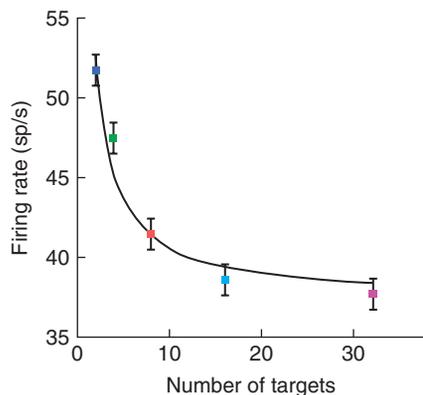
These observations indicate that value modulation of sensory-motor processing in parietal cortex, and presumably other areas that contribute to decision-making, is relative and not absolute, in contrast with value signals in OFC. Consistent with this notion, Platt and colleagues found that LIP neurons 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 number of elements in the array increased (Figure 29.7). Similar findings have been reported for neurons in the superior colliculus by Basso and Wurtz (1997).

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 reticulata (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



f0070 **FIGURE 29.7** Normalization of neuronal activity in LIP by target number. An array of irrelevant dots was displayed in the response fields of neurons in LIP while monkeys waited to shift gaze in the opposite direction. For a subpopulation of neurons, firing rate systematically decreased with increasing number of dots. Divisive normalization by target number may contribute to relative value scaling of target-related activity in LIP.

attention (Horvitz, 2000), it is possible that reward modulation of neuronal activity in brain areas associated with visual orienting might actually reflect changes in attention, and *vice versa* (Maunsell, 2004). In other words, attention and value are naturally linked and thus difficult to disentangle either behaviorally or neurophysiologically.

p0350 In an initial attempt to address this issue, Bendiksbj 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 (Bendiksbj 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 – 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 Bendiksbj 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.

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## EVALUATION OF EVENTS AND ACTIONS IN POSTERIOR CINGULATE CORTEX

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### Anatomical, Clinical, and Neuroimaging Significance of Posterior Cingulate Cortex

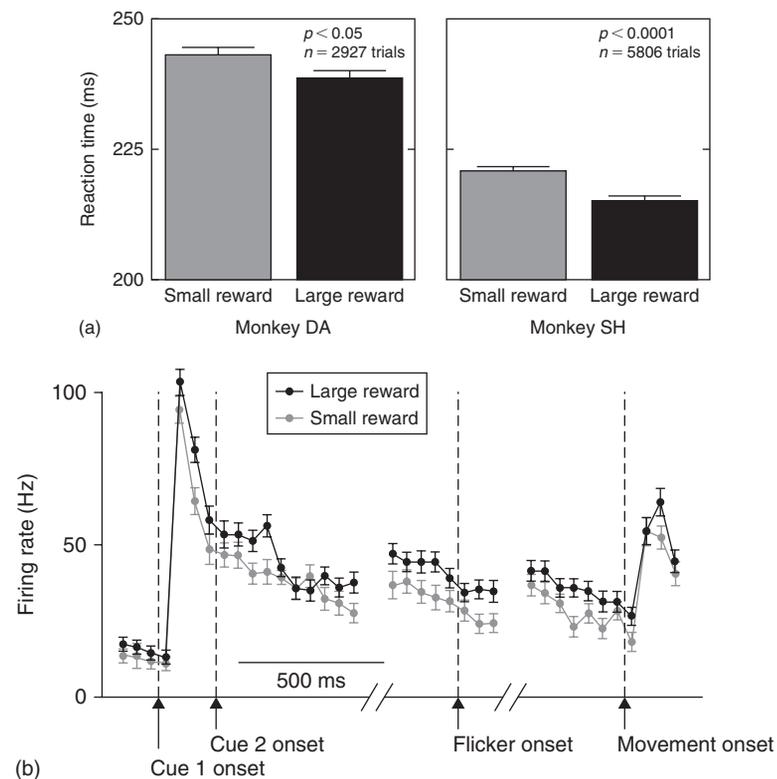
s0130

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.

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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; Baleyrier 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 Mauguier, 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 Mauguier, 1980; Pandya *et al.*, 1981; Vogt and Pandya, 1987; Cavada and Goldman-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.

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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 associated 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

p0390

## V. THE NEURAL MECHANISMS FOR CHOICE

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.

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

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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; Preusschoff *et al.*, 2006). Moreover, choosing a risky option activates the dorsal striatum, posterior cingulate cortex, and precuneus (Dickhaut *et al.*, 2003) as well as amygdale (Hsu *et al.*, 2005) and insula (Huettel *et al.*, 2006).

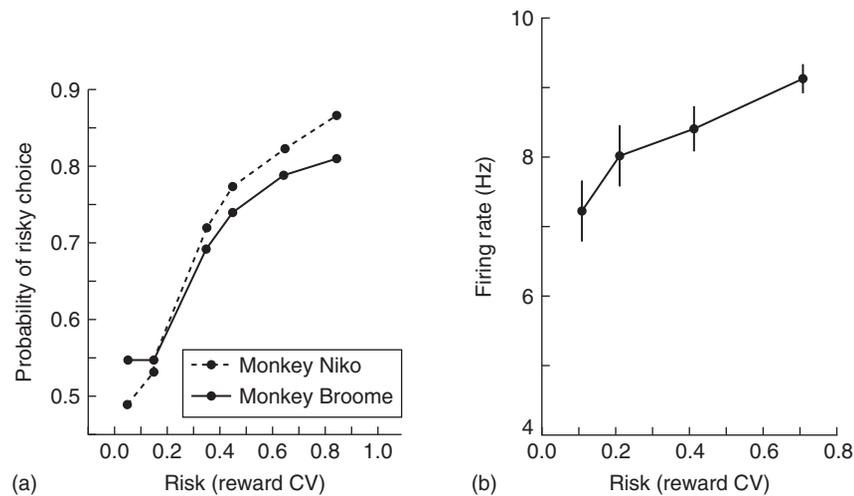
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These observations suggest that the neural mechanisms that bind value to events and action must also be sensitive to risk if these processes contribute to choice. To test this idea, McCoy and Platt (2005) used a visual gambling task to assess whether 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

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### s0140 Neurophysiological Evidence that CGp Plays a Role in Evaluating Behavioral Events

p0410 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 (Kalia 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).



**FIGURE 29.9** CGp neurons report the subjective value of a gamble. Monkeys chose between a risky option and a safe option matched for expected value while neuronal activity in posterior cingulate cortex was recorded. (a) Two monkeys preferred the risky option, and preference increased with increasing risk. (b) The firing rate preceding reward delivery increased with increasing risk, thus matching the subjective preferences of the monkeys.

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.

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.

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### NEURO-COGNITIVE MODELS OF CHOICE

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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

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, Bendiksy 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 (Bendiksy 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.)

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In conclusion, value signals in sensory areas might underlie perceptual attention.

p0490 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.

p0500 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.

### s0190 “Goods-based” and “Actions-based” Models of Economic Choice

p0510 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.

p0520 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  $V(a_1, a_2, \dots)$  of multiple arguments  $a_1, a_2, \dots$  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, p0530 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,

economic choice is fundamentally choice between actions.

### s0200 Comparing Goods-based and Actions-based Models

p0540 *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.

p0550 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 Hikosake, 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.

p0560 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 place in the abstract representation of goods. The key tenet of the good-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 LIP (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 Tranel, 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.

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## CONCLUSION

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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 brain areas like the parietal cortex.

p0610

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.

## References

- Amador, N., Schlag-Rey, M., and Schlag, J. (2000). Reward-predicting and reward-detecting neuronal activity in the primate supplementary eye field. *J. Neurophysiol.* 84, 2166–2170.
- Andersen, R.A., Asanuma, C., Essick, G., and Siegel, R.M. (1990). Corticocortical connections of anatomically and physiologically defined subdivisions within the inferior parietal lobule. *J. Comp. Neurol.* 296, 65–113.
- Arana, F.S., Parkinson, J.A., Hinton, E. *et al.* (2003). Dissociable contributions of the human amygdala and orbitofrontal cortex to incentive motivation and goal selection. *J. Neurosci.* 23, 9632–9638.
- Arnaud, A. and Nichole, P. (1982 (1662)). *The Art of Thinking: Port-Royal Logic*. Indianapolis, IN: Bobbs-Merrill.
- Balan, P.F. and Gottlieb, J. (2006). Integration of exogenous input into a dynamic salience map revealed by perturbing attention. *J. Neurosci.* 26, 9239–9249.
- Baleydier, C. and Mauguiere, F. (1980). The duality of the cingulate gyrus in monkey. Neuroanatomical study and functional hypothesis. *Brain* 103, 525–554.
- Barbas, H. and Mesulam, M.M. (1981). Organization of afferent input to subdivisions of area 8 in the rhesus monkey. *J. Comp. Neurol.* 200, 407–431.
- Barbas, H. and Mesulam, M.M. (1985). Cortical afferent input to the principalis region of the rhesus monkey. *Neuroscience* 15, 619–637.
- Barbas, H. and Pandya, D.N. (1989). Architecture and intrinsic connections of the prefrontal cortex in the rhesus monkey. *J. Comp. Neurol.* 286, 353–375.
- Basso, M.A. and Wurtz, R.H. (1997). Modulation of neuronal activity by target uncertainty. *Nature* 389, 66–69.
- Bechara, A., Tranel, D., Damasio, H. and Damasio, A.R. Failure to respond autonomically to anticipated future outcomes following damage to prefrontal cortex. *Cerebral Cortex*, 6, 215–225.
- Bendiksy, M.S. and Platt, M.L. (2006). Neural correlates of reward and attention in macaque area LIP. *Neuropsychologia* 44, 2411–2420.
- Berman, R.A., Colby, C.L., Genovese, R. *et al.* (1999). Cortical networks subserving pursuit and saccadic eye movements in humans: an fMRI study. *Human Brain Mapp.* 8, 125–209.
- Bernheim, B.D. and Rangel, A. (2004). Addiction and cue-triggered decision processes. *Am. Econ. Rev.* 94, 1558–1590.
- Bickel, W.K., Odum, A.L., and Madden, G.J. (1999). Impulsivity and cigarette smoking: delay discounting in current, never, and ex-smokers. *Psychopharmacology* 146, 447–454.
- Blatt, G.J., Andersen, R.A., and Stoner, G.R. (1990). Visual receptive field organization and cortico-cortical connections of the lateral intraparietal area (area LIP) in the macaque. *J. Comp. Neurol.* 299, 421–445.
- Braak, H., Braak, E., Yilmazer, D. *et al.* (1996). Pattern of brain destruction in Parkinson's and Alzheimer's diseases. *J. Neural Transm.* 103, 455–490.
- Bundesen, C. (1990). A theory of visual attention. *Psychological Rev.* 97, 523–547.
- Cammalleri, R., Gangitano, M., D'Amelio, M. *et al.* (1996). Transient topographical amnesia and cingulate cortex damage: a case report. *Neuropsychologia* 34, 321–326.
- Carmichael, S.T. and Price, J.L. (1994). Architectonic subdivision of the orbital and medial prefrontal cortex in the macaque monkey. *J. Comp. Neurol.* 346, 366–402.
- Carmichael, S.T. and Price, J.L. (1995). Sensory and premotor connections of the orbital and medial prefrontal cortex of macaque monkeys. *J. Comp. Neurol.* 363, 642–664.
- Cavada, C. and Goldman-Rakic, P.S. (1989a). Posterior parietal cortex in rhesus monkey: II. Evidence for segregated corticocortical networks linking sensory and limbic areas with the frontal lobe. *J. Comp. Neurol.* 287, 422–445.
- Cavada, C. and Goldman-Rakic, P.S. (1989b). Posterior parietal cortex in rhesus monkey: I. Parcellation of areas based on distinctive limbic and sensory corticocortical connections. *J. Comp. Neurol.* 287, 393–421.

- Cavada, C., Company, T., Tejedor, J. *et al.* (2000). The anatomical connections of the macaque monkey orbitofrontal cortex. A review. *Cerebral Cortex* 10, 220–242.
- Cheney, D.L. and Seyfarth, R.M. (1990). *How Monkeys See the World: Inside the Mind of Another Species*. Chicago, IL: Chicago University Press, x 377.
- Choi, S., Fisman, R., Gale, D., and Kariv, S. (2008). Consistency and heterogeneity of individual behavior under uncertainty. *Am. Econ. Rev.* 97, 1858–1876.
- Coe, B., Tomihara, K., Matsuzawa, M., and Hikosaka, O. Visual and anticipatory bias in three cortical eye fields of the monkey during an adaptive decision-making task. *J. Neurosci.*, 22, 5081–5090.
- Colby, C.L. and Olson, C.R. (1999). Spatial cognition. In: M.J. Zigmond, F.E. Bloom, S.C. Landis. *et al.* (eds), *Fundamental Neuroscience*. San Diego, CA: Academic Press, pp. 1363–1383.
- Colby, C.L., Duhamel, J.R., and Goldberg, M.E. (1996). Visual, pre-saccadic, and cognitive activation of single neurons in monkey lateral intraparietal area. *J. Neurophysiol.* 76, 2841–2852.
- Damasio, H., Grabowski, T., Frank, R. *et al.* (1994). The return of Phineas Gage: clues about the brain from the skull of a famous patient. *Science* 264, 1102–1105.
- Dean, H.L. and Platt, M.L. (2006). Allocentric spatial referencing of neuronal activity in macaque posterior cingulate cortex. *J. Neurosci.* 26, 1117–1127.
- Dean, H.L., Crowley, J.C., and Platt, M.L. (2004). Visual and saccade-related activity in macaque posterior cingulate cortex. *J. Neurophysiol.* 92, 3056–3068.
- Deaner, R.O., Khera, A.V., and Platt, M.L. (2005). Monkeys pay per view: adaptive valuation of social images by rhesus macaques. *Curr. Biol.* 15, 543–548.
- Desimone, R. and Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.* 18, 193–222.
- Dickhaut, J., McCabe, K., Nagode, J.C. *et al.* (2003). The impact of the certainty context on the process of choice. *Proc. Natl Acad. Sci. USA* 100, 3536–3541.
- Dickinson, A. and Balleine, B.W. (2002). The role of learning in the operation of motivational systems. In: C.R. Gallistel (ed.), *Learning, Motivation and Emotion. Steven's Handbook of experimental Psychology*, Vol. 3. New York, NY: John Wiley & Sons, pp. 497–533.
- Dorris, M.C. and Glimcher, P.W. (2004). Activity in posterior parietal cortex is correlated with the relative subjective desirability of action. *Neuron* 44, 365–378.
- Fellows, L.K. and Farah, M.J. (2007). The role of ventromedial prefrontal cortex in decision making: judgment under uncertainty or judgment per se? *Cerebral Cortex* 17, 2669–2674.
- Feierstein, C.E., Quirk, M.C., Uchida, N. *et al.* (2006). Representation of spatial goals in rat orbitofrontal cortex. *Neuron* 51, 495–507.
- Fletcher, W.A. (1994). Ophthalmological aspects of Alzheimer's disease. *Curr. Opin. Ophthalmol.* 5, 38–44.
- Flitman, S., O'Grady, J., Cooper, V., and Grafman, J. (1997). PET imaging of maze processing. *Neuropsychologia* 35, 409–420.
- Fodor, J.A. (1983). *The Modularity of Mind: An Essay on Faculty Psychology*. Cambridge, MA: MIT Press.
- Gabriel, M. (1990). Functions of anterior and posterior cingulate cortex during avoidance learning in rabbits. *Prog. Brain Res.* 85, 467–482, discussion 482–483.
- Gabriel, M., Vogt, B.A., Kubota, Y. *et al.* (1991). Training-stage related neuronal plasticity in limbic thalamus and cingulate cortex during learning: a possible key to mnemonic retrieval. *Behav. Brain Res.* 46, 175–185.
- Ghaem, O., Mellet, E., Crivello, F. *et al.* (1997). Mental navigation along memorized routes activates the hippocampus, precuneus, and insula. *NeuroReport* 8, 739–744.
- Glimcher, P.W., Dorris, M.C., and Bayer, H.M. (2005). Physiological utility theory and the neuroeconomics of choice. *Games Econ. Behav.* 52, 213–256.
- Gnadt, J.W. and Andersen, R.A. (1988). Memory related motor planning activity in posterior parietal cortex of macaque. *Exp. Brain Res.* 70, 216–220.
- Gold, J.I. and Shadlen, M.N. (2001). Neural computations that underlie decisions about sensory stimuli. *Trends Cogn. Sci.* 5, 10–16.
- Goldberg, M.E., Colby, C.L., and Duhamel, J.R. (1990). Representation of visuomotor space in the parietal lobe of the monkey. *Cold Spring Harbour Symp. Quant. Biol.* 55, 729–739.
- Goldberg, M.E., Bisley, J., Powell, K.D. *et al.* (2002). The role of the lateral intraparietal area of the monkey in the generation of saccades and visuospatial attention. *Ann. N Y Acad. Sci.* 956, 205–215.
- Goodall, E.B. and Carey, R.J. (1975). Effects of d- versus l-amphetamine, food deprivation, and current intensity on self-stimulation of the lateral hypothalamus, substantia nigra, and medial frontal cortex of the rat. *J. Comp. Physiol. Psychol.* 89, 1029–1045.
- Gottlieb, J.P., Kusunoki, M., and Goldberg, M.E. (1998). The representation of visual salience in monkey parietal cortex. *Nature* 391, 481–484.
- Grace, R.C. (1993). Violations of transitivity: implications for a theory of contextual choice. *J. Exp. Anal. Behav.* 60, 185–201.
- Graybiel, A.M. (2005). The basal ganglia: learning new tricks and loving it. *Curr. Opin. Neurobiol.* 15, 638–644.
- Hrdy, S.B. and Whitten, P.L. (1987). Patterning of sexual activity. In: B.B. Smuts, R.M. Seyfarth, R.W. Wrangham, and T.T. Struhsake (eds), *Primate Societies*. Chicago, IL: University of Chicago Press, pp. 370–384.
- Hayden, B.Y. and Platt, M.L. (2007). Temporal discounting predicts risk sensitivity in rhesus macaques. *Curr. Biol.* 17, 49–53.
- Hayden, B.Y., Parikh, P.C., Deaner, R.O., and Platt, M.L. (2007). Economic principles motivating social attention in humans. *Proc. Biol. Sci.* 274, 1751–1756.
- Heeger, D.J. (1993). Modeling simple-cell direction selectivity with normalized, half-squared, linear operators. *J. Neurophysiol.* 70, 1885–1898.
- Hikosaka, O., Nakamura, K., and Nakahara, H. (2006). Basal ganglia orient eyes to reward. *J. Neurophysiol.* 95, 567–584.
- Hof, P.R., Archin, N., Osmand, A.P. *et al.* (1993). Posterior cortical atrophy in Alzheimer's disease: analysis of a new case and re-evaluation of a historical report. *Acta Neuropathol.* 86, 215–223.
- Hof, P.R., Vogt, B.A., Bouras, C., and Morrison, J.H. (1997). Atypical form of Alzheimer's disease with prominent posterior cortical atrophy: a review of lesion distribution and circuit disconnection in cortical visual pathways. *Vision Res.* 37, 3609–3625.
- Hopfinger, J.B., Buonocore, M.H., and Mangun, G.R. (2000). The neural mechanisms of top-down attentional control. *Nat. Neurosci.* 3, 284–291.
- Hopfinger, J.B., Woldorff, M.G., Fletcher, E.M., and Mangun, G.R. (2001). Dissociating top-down attentional control from selective perception and action. *Neuropsychologia* 39, 1277–1291.
- Horvitz, J.C. (2000). Mesolimbocortical and nigrostriatal dopamine responses to salient non-reward events. *Neuroscience* 96, 651–656.
- Huettel, S.A., Stowe, C.J., Gordon, E.M. *et al.* (2006). Neural signatures of economic preferences for risk and ambiguity. *Neuron* 49, 765–775.
- Hsu, M., Bhatt, M., Adolphs, R. *et al.* (2005). Neural systems responding to degrees of uncertainty in human decision-making. *Science* 310, 1680–1683.

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- Ikeda, T. and Hikosaka, O. (2003). Reward-dependent gain and bias of visual responses in primate superior colliculus. *Neuron* 39, 693–700.
- Ito, S., Stuphorn, V., Brown, J.W., and Schall, J.D. (2003). Performance monitoring by the anterior cingulate cortex during saccade countermanding. *Science* 302, 120–122.
- Kable, J.W. and Glimcher, P.W. (2007). The neural correlates of subjective value during intertemporal choice. *Nat. Neurosci.* 10, 1625–1633.
- Kalia, M. and Whitteridge, D. (1973). The visual areas in the splenic sulcus of the cat. *J. Physiol.* 232, 275–283.
- Kandel, E.R., Schwartz, J.H., and Jessell, T.M. (eds) (2000). *Principles of Neural Science*, Vol. XLI. New York, NY: McGraw-Hill.
- Katayama, K., Takahashi, N., Ogawara, K., and Hattori, T. (1999). Pure topographical disorientation due to right posterior cingulate lesion. *Cortex* 35, 279–282.
- Kawagoe, R., Takikawa, Y., and Hikosaka, O. (1998). Expectation of reward modulates cognitive signals in the basal ganglia. *Nat. Neurosci.* 1, 411–416.
- Kim, Y.H., Gitelman, D.R., Nobre, A.C. et al. (1999). The large-scale neural network for spatial attention displays multifunctional overlap but differential asymmetry. *NeuroImage* 9, 269–277.
- Koenigs, M. and Tranel, D. (2007). Irrational economic decision-making after ventromedial prefrontal damage: evidence from the Ultimatum Game. *J. Neurosci.* 27, 951–956.
- Klein, J.T., Deaner, R.O., and Platt, M.L. (2008). Neural correlates of social target value in macaque parietal cortex. *Curr. Biol.* 18, 419–424.
- Kreps, D.M. (1990). *A Course in Microeconomic Theory*. Princeton, NJ: Princeton University Press.
- Kuhnen, C.M. and Knutson, B. (2005). The neural basis of financial risk taking. *Neuron* 47, 763–770.
- Leon, M.I. and Shadlen, M.N. (1999). Effect of expected reward magnitude on the response of neurons in the dorsolateral prefrontal cortex of the macaque. *Neuron* 24, 415–425.
- Maddock, R.J. (1999). The retrosplenial cortex and emotion: new insights from functional neuroimaging of the human brain. *Trends Neurosci.* 22, 310–316.
- Maddock, R.J., Garrett, A.S., and Buonocore, M.H. (2003). Posterior cingulate cortex activation by emotional words: fMRI evidence from a valence decision task. *Human Brain Mapp.* 18, 30–41.
- Maratos, E.J., Dolan, R.J., Morris, J.S. et al. (2001). Neural activity associated with episodic memory for emotional context. *Neuropsychologia* 39, 910–920.
- Maunsell, J.H. (2004). Neuronal representations of cognitive state: reward or attention? *Trends Cogn. Sci.* 8, 261–265.
- Mazur, J.E. and Coe, D. (1987). Tests of transitivity in choices between fixed and variable reinforcer delays. *J. Exp. Anal. Behav.* 47, 287–297.
- McCoy, A.N. and Platt, M.L. (2005). Risk-sensitive neurons in macaque posterior cingulate cortex. *Nat. Neurosci.* 8, 1220–1227.
- McCoy, A.N., Crowley, J.C., Haghghian, G. et al. (2003). Reward signals in posterior cingulate cortex. *Neuron* 40, 1031–1040.
- Mesulam, M.M., Nobre, A.C., Kim, Y.H. et al. (2001). Heterogeneity of cingulate contributions to spatial attention. *NeuroImage* 13, 1065–1072.
- Minamimoto, T., Hori, Y., and Kimura, M. (2005). Complementary process to response bias in the centromedian nucleus of the thalamus. *Science* 308, 1798–1801.
- Minoshima, S., Giordani, B., Barent, S. et al. (1997). Metabolic reduction in the posterior cingulate cortex in very early Alzheimer's disease. *Ann. Neurol.* 42, 85–94.
- Morecraft, R.J., Geula, C., and Mesulam, M.M. (1993). Architecture of connectivity within a cingulo-fronto-parietal neurocognitive network for directed attention. *Arch. Neurol.* 50, 279–284.
- Muller-Preuss, P. and Jürgens, U. (1976). Projections from the “cingular” vocalization area in the squirrel monkey. *Brain Res.* 103, 29–43.
- Mussa-Ivaldi, F.A. and Bizzi, E. (2000). Motor learning through the combination of primitives. *Phil. Trans. R. Soc. Lond. B*, 355, 1755–1769.
- Navarick, D.J. and Fantino, E. (1972). Transitivity as a property of choice. *J. Exp. Anal. Behav.* 18, 389–401.
- Niki, H. and Watanabe, M. (1979). Prefrontal and cingulate unit activity during timing behavior in the monkey. *Brain Res.* 171, 213–224.
- O'Doherty, J.P. (2004). Reward representations and reward-related learning in the human brain: insights from neuroimaging. *Curr. Opin. Neurobiol.* 14, 769–776.
- Olson, C.R. and Musil, S.Y. (1992). Posterior cingulate cortex: sensory and oculomotor properties of single neurons in behaving cat. *Cerebral Cortex* 2, 485–502.
- Olson, C.R., Musil, S.Y., and Goldberg, M.E. (1996). Single neurons in posterior cingulate cortex of behaving macaque: eye movement signals. *J. Neurophysiol.* 76, 3285–3300.
- Padoa-Schioppa, C. (2007). Orbitofrontal cortex and the computation of economic value. *Ann. NY Acad. Sci.* 1121, 232–253.
- Padoa-Schioppa, C. and Assad, J.A. (2006). Neurons in orbitofrontal cortex encode economic value. *Nature* 441, 223–226.
- Padoa-Schioppa, C. and Assad, J.A. (2008). The representation of economic value in the orbitofrontal cortex is invariant for changes of menu. *Nat. Neurosci.* 11, 95–102.
- Padoa-Schioppa, C., Jandolo, L., and Visalberghi, E. (2006). Multi-stage mental process for economic choice in capuchins. *Cognition* 99, B1–B13.
- Pandya, D.N., van Hoesen, G.W., and Mesulam, M.M. (1981). Efferent connections of the cingulate gyrus in the rhesus monkey. *Exp. Brain Res.* 42, 319–330.
- Pasquier, F. and Petit, H. (1997). Frontotemporal dementia: its rediscovery. *Eur. Neurol.* 38, 1–6.
- Paton, J.J., Belova, M.A., Morrison, S.E., and Salzman, C.D. (2006). The primate amygdala represents the positive and negative value of visual stimuli during learning. *Nature* 439, 865–870.
- Pearce, J.M. and Hall, G. (1980). A model for Pavlovian learning: variations in the effectiveness of conditioned but not of unconditioned stimuli. *Psychological Rev.* 87, 532–552.
- Pine, D.S., Grun, J., Maguire, E.A. et al. (2002). Neurodevelopmental aspects of spatial navigation: a virtual reality fMRI study. *NeuroImage* 15, 396–406.
- Pinker, S. (1997). *How the Mind Works*, Vol. XII. New York, NY: Norton.
- Platt, M.L. and Glimcher, P.W. (1997). Responses of intraparietal neurons to saccadic targets and visual distractors. *J. Neurophysiol.* 78, 1574–1589.
- Platt, M.L. and Glimcher, P.W. (1999). Neural correlates of decision variables in parietal cortex. *Nature* 400, 233–238.
- Powell, E.W. (1978). The cingulate bridge between allocortex, isocortex and thalamus. *Anat. Rec.* 190, 783–793.
- Price, J.L. (2007). Definition of the orbital cortex in relation to specific connections with limbic and visceral structures, and other cortical regions. *Ann NY Acad. Sci.* 1121, 54–71.
- Rachlin, H. (2000). *The Science of Self-control*. Cambridge, MA: Harvard University Press.
- Rahman, S., Sahakian, B.J., Hodges, J.R. et al. (1999). Specific cognitive deficits in mild frontal variant of frontotemporal dementia. *Brain* 122, 1469–1493.
- Roesch, M.R. and Olson, C.R. (2003). Impact of expected reward on neuronal activity in prefrontal cortex, frontal and supplementary eye fields and premotor cortex. *J. Neurophysiol.* 90, 1766–1789.

## V. THE NEURAL MECHANISMS FOR CHOICE

- Roesch, M.R. and Olson, C.R. (2005). Neuronal activity in primate orbitofrontal cortex reflects the value of time. *J. Neurophysiol.* 94, 2457–2471.
- Roesch, M.R., Taylor, A.R., and Schoenbaum, G. (2006). Encoding of time-discounted rewards in orbitofrontal cortex is independent of value representation. *Neuron* 51, 509–520.
- Roitman, J.D., Brannon, E.M., and Platt, M.L. (2007). Monotonic coding of numerosity in macaque lateral intraparietal area. *PLoS Biol* 5, e208.
- Rolls, E.T., Sienkiewicz, Z.J., and Yaxley, S. (1989). Hunger modulates the responses to gustatory stimuli of single neurons in the caudolateral orbitofrontal cortex of the macaque monkey. *Eur. J. Neurosci.* 1, 53–60.
- Salzman, C.D., Belova, M.A., and Paton, J.J. (2005). Beetles, boxes and brain cells: neural mechanisms underlying valuation and learning. *Curr. Opin. Neurobiol.* 15, 721–729.
- Sato, M. and Hikosaka, O. (2002). Role of primate substantia nigra pars reticulata in reward-oriented saccadic eye movement. *J. Neurosci.* 22, 2363–2373.
- Schwartz, O. and Simoncelli, E.P. (2001). Natural signal statistics and sensory gain control. *Nat. Neurosci.* 4, 819–825.
- Selemon, L.D. and Goldman-Rakic, P.S. (1988). Common cortical and subcortical targets of the dorsolateral prefrontal and posterior parietal cortices in the rhesus monkey: evidence for a distributed neural network subserving spatially guided behavior. *J. Neurosci.* 8, 4049–4068.
- Shafir, S. (1994). Intransitivity of preferences in honey bees: support for “comparative” evaluation of foraging options. *Animal Behav.* 48, 55–67.
- Shidara, M. and Richmond, B.J. (2002). Anterior cingulate: single neuronal signals related to degree of reward expectancy. *Science* 296, 1709–1711.
- Sikes, R.W. and Vogt, B.A. (1992). Nociceptive neurons in area 24 of rabbit cingulate cortex. *J. Neurophysiol.* 68, 1720–1732.
- Simon, H.A. (1962). The architecture of complexity. *Proc. Am. Phil. Soc.* 106, 467–482.
- Skinner, B.F. (1953). *Science and Human Behavior*. New York, NY: Macmillan.
- Small, D.M., Zatorre, R.J., Dagher, A. *et al.* (2001). Changes in brain activity related to eating chocolate: from pleasure to aversion. *Brain* 124, 1720–1733.
- Small, D.M., Gitelman, D.R., Gregory, M.D. *et al.* (2003). The posterior cingulate and medial prefrontal cortex mediate the anticipatory allocation of spatial attention. *NeuroImage* 18, 633–641.
- Spence, S.J., Silverman, J.A., and Corbett, D. (1985). Cortical and ventral tegmental systems exert opposing influences on self-stimulation from the prefrontal cortex. *Behav. Brain Res.* 17, 117–124.
- Stuphorn, V., Taylor, T.L., and Schall, J.D. (2000). Performance monitoring by the supplementary eye field. *Nature* 408, 857–860.
- Sugrue, L.P., Corrado, G.S., and Newsome, W.T. (2004). Matching behavior and the representation of value in the parietal cortex. *Science* 304, 1782–1787.
- Sutton, R.S. and Barto, A.G. (1998). *Reinforcement Learning: An Introduction*, Vol. XVIII. Cambridge, MA: MIT Press.
- Takahashi, N., Kawamura, M., Shiota, J. *et al.* (1997). Pure topographic disorientation due to right retrosplenial lesion. *Neurology* 49, 464–469.
- Thorpe, S.J., Rolls, E.T., and Maddison, S. (1983). The orbitofrontal cortex: neuronal activity in the behaving monkey. *Exp. Brain Res.* 49, 93–115.
- Tremblay, L. and Schultz, W. (1999). Relative reward preference in primate orbitofrontal cortex. *Nature* 398, 704–708.
- Tversky, A. (1969). The intransitivity of preferences. *Psychological Rev.* 76, 31–48.
- Vogt, B.A. and Pandya, D.N. (1987). Cingulate cortex of the rhesus monkey: II. Cortical afferents. *J. Comp. Neurol.* 262, 271–289.
- Wallis, J.D. (2007). Orbitofrontal cortex and its contribution to decision-making. *Annu. Rev. Neurosci.* 30, 31–56.
- Watanabe, K., Lauwereyns, J., and Hikosaka, O. (2003). Neural correlates of rewarded and unrewarded eye movements in the primate caudate nucleus. *J. Neurosci.* 23, 10052–10057.
- Wolpert, D.M. and Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nat. Neurosci.* 3(Suppl.), 1212–1217.
- Yamasaki, H., LaBar, K.S., and McCarthy, G. (2002). Dissociable prefrontal brain systems for attention and emotion. *Proc. Natl Acad. Sci. USA* 99, 11447–11451.
- Yeterian, E.H. and van Hoesen, G.W. (1978). Cortico-striate projections in the rhesus monkey: the organization of certain cortico-caudate connections. *Brain Res.* 139, 43–63.