CHAPTER

8

The Computation of Stimulus Values in Simple Choice

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OUTLINE

INTRODUCTION

Neuroeconomics combines methods and theories from neuroscience, psychology, economics, and computer science to study three questions: (i) what are the variables computed by the brain to make different types of decisions; (ii) how does the underlying neurobiology implement and constrain these computations; (iii) what are the implications of this knowledge for understanding behavior and well-being? Neuroeconomics seeks to produce detailed computational and neurobiological accounts of the choice process that can serve as a common foundation for understanding human behavior across the natural and social sciences (Clithero *et al.*, 2008; Fehr and Rangel, 2011; Glimcher, 2011; Rangel *et al.*, 2008; Wilson, 1998).

A basic question is how does the brain make *simple choices*, such as choosing between an apple and an orange. Much effort has been devoted to studying whether the brain makes these choices by computing and comparing value signals, to characterizing the computational and neurobiological properties of the various processes involved, and to understanding how they influence choices. This research agenda is based on the belief that simple choice provides a good test bed for the systematic study of neuroeconomic questions, and that some of its essential computational and neurobiological features are likely to be preserved in more complex decisions. As is illustrated in many of the other chapters in this volume, so far this has proven a reasonably accurate assumption.

Simple choices are more complex and interesting than they might seem. They involve the parallel computation of several distinct value signals, as well as the dynamic integration and comparison of those value signals in order to elicit the *motor response*, or movement, necessary to execute the decision (e.g., reach left and grab the orange, or reach right and grab the apple).

This chapter provides an introduction to what is known about how the brain computes what are often called *stimulus values*. There is now some evidence that during simple choice, the brain computes and

represents these stimulus values, a measure of the expected benefit of consuming the different options, independently of the action costs required to get them. In contrast, *action costs* measure the effort or unpleasantness associated with executing an action, independently of the expected benefits that those actions might generate. For example, if a hungry rat needs to execute ten painful nose pokes to get access to a food port, the action costs are the effort associated with the nose pokes, the stimulus value is the hedonic response from consuming the food, and the net value of taking the action is given by the stimulus values minus the action costs. Although stimulus values are only one of several kinds of value signals hypothesized to be computed at the time of decision, they have received much attention because there is growing evidence that in many circumstances they are the key drivers of choice. This occurs, for example, when the action costs associated with acquiring the options are negligible relative to the benefits from consuming them, or when the action costs of the options under consideration are identical.

The chapter has several goals. First, it provides an introduction to the study of stimulus valuation for those new to neuroeconomics. This includes a thorough review of the methodological issues involved in identifying stimulus value signals in the brain, and some insights into the relative merits of alternative experimental approaches. Second, the chapter provides a discussion of the research frontier in this area, including the body of findings for which there is a degree of consensus, as well as some key areas of disagreement. Third, the chapter emphasizes the importance of computational models in neuroeconomics. To make this point explicitly, it shows how a fully specified computational model of simple choice is critical for making sense of seemingly contradictory findings in the literature. It should be noted that many of the issues engaged here are discussed in further detail in Chapter 22.

It is important to emphasize several limitations in the scope of the chapter. It discusses computational modeling, human functional magnetic resonance imaging (fMRI), and non-human primate neurophysiology studies, but it does not cover related rodent experiments. There are, however, several excellent reviews on this topic (McDannald *et al.*, 2012; Schoenbaum *et al.*, 2009). The chapter also does not discuss feedback and reward learning issues, instead focusing on what happens at the time of decision, given all preceding learning. See Chapters 15–18, for value learning. The chapter only considers choices that are made using the goal-directed control system, as opposed to the competing habitual and Pavlovian controllers. These other types of choices are taken up explicitly in Chapter 21. As a result, the chapter only discusses choice situations that are not *over-trained*, in the sense that they are relatively novel to the subjects. Finally, it should be noted that given the size of the relevant literature, and the pedagogical aspirations of the chapter, it focuses on depth at the expense of breadth.

THEORY: A COMPUTATIONAL MODEL OF SIMPLE CHOICE

Consider the choice task depicted in Figure 8.1A, which illustrates a widely used class of paradigms. On every trial the subject is shown a consumption stimulus (for example a tasty food), as well as the amount of effort required to get it. In order to get the food the subject might need to squeeze a handgrip (a plastic cylinder containing an air tube that can be squeezed, compressing the air tube in a way that allows accurate measurement of physical effort exerted) with a minimum amount of force for a minimum length of time. The subject needs to decide whether he wants to get the food in exchange for that effort, or get nothing but do no work. The decision is indicated by a left-hand (=Yes) or right-hand (=No) button press. If the subject chooses "Yes," then he needs to carry out the effort in order to get the consumption item. Subjects are allowed to indicate their choice whenever they are ready.

A large body of behavioral data has shown that these types of tasks lead to psychometric choice curves that are consistent with the logistic choice model (Luce, 1959; McFadden, 2001). As illustrated in Figure 8.1B, the probability of saying "Yes" increases with the subjective value of the consumption good, and decreases with the action costs.

Figure 8.1C describes a simple computational model of the task. It describes the variables that are computed at the time of choice, and how they interact with each other to affect behavior, without specifying the details of how they are implemented in the brain. The model has two key components: value signals and a comparator process.

Consider the valuation process first. The model assumes that three distinct value signals are computed from the time the choice screen appears to the time a decision is made. First, there are stimulus value (SV) signals that measure the expected subjective value of consuming the stimulus, independently of the action required to acquire it. If delivery of the stimulus is probabilistic or delayed, the SV signal takes this into account, by weighting potential outcomes according to their probability, and temporally discounting delayed rewards. Thus, an unlikely reward delivered far in the future is assigned a lower SV than an otherwise more likely and proximate one. Similarly, if the action gives the subject the right to buy the good at a certain price, the price is also part of the SV. Risk, delay, and price

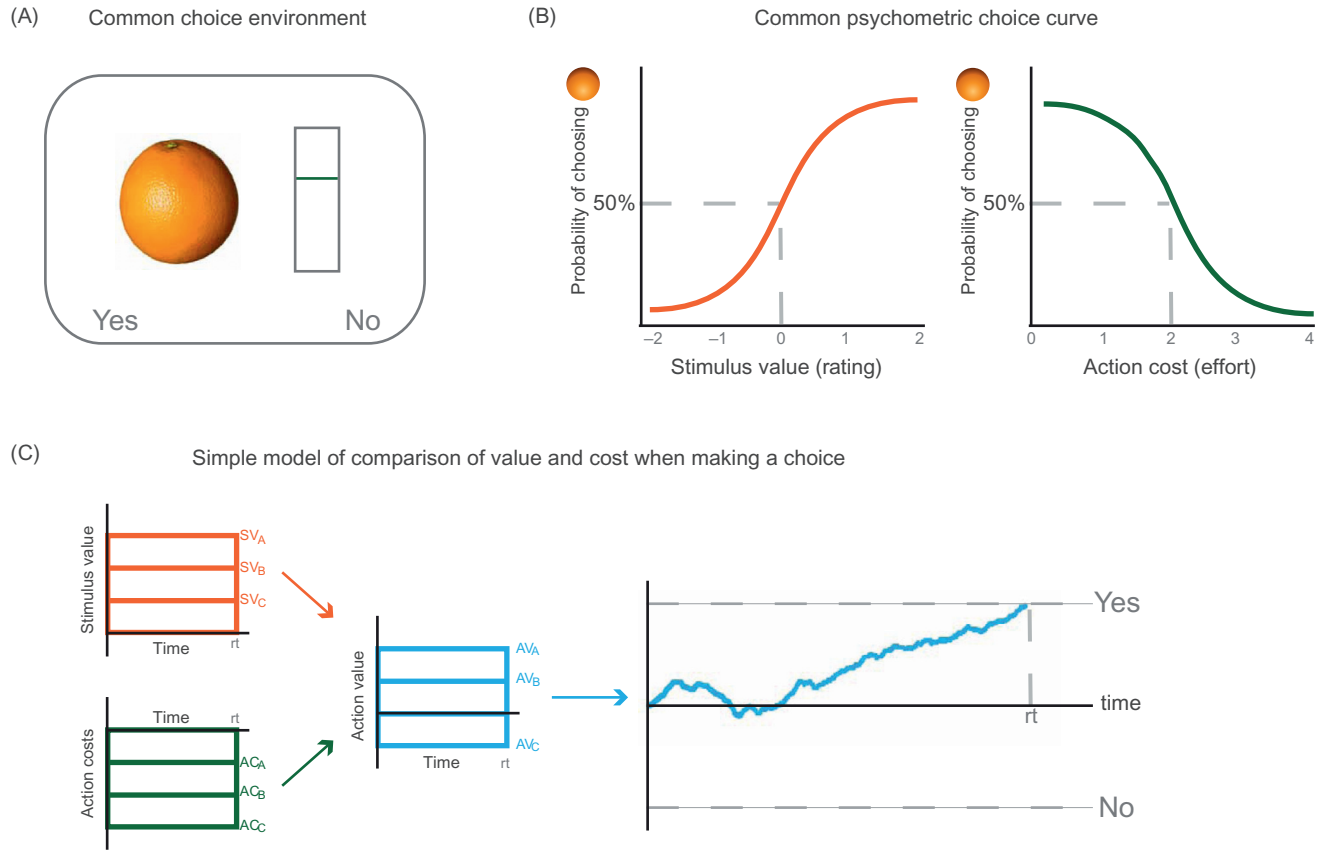

FIGURE 8.1 (A) A common choice task for subjects in experiments is a simple Yes/No decision. Here, the subject can exert an amount of effort (indicated by the green line on the right) and receive an orange (indicated on the left). Responses are provided by button press (left = YES, right = NO). (B) Psychometric choice curves. If choice data are collected and a choice function is estimated assuming a logistic fit, subjects will generally have a probablility of saying "YES" that is increasing in the stimulus value of the orange (orange curve on left), and decreasing in the action cost of obtaining the orange (green curve on right). (C) A simple choice model that integrates stimulus values and action costs to compute stimulus values. Consider three different goods, A, B, and C, with different stimulus values and action costs. Once they are combined, option A has the greatest action value of the three (given its highest stimulus value and lowest action cost). The model also assumes a noisy-drift process (right), whereby a subject's decision-making process accumulates information until a sufficient threshold (grey lines) is crossed. In this case, the subject chose "YES".

are inherent properties of the stimulus, and thus are integral to the SV computation. Second, there are action cost (AC) signals that reflect the subjective value of taking the action required to get the item, independently of the benefits generated by the stimulus. These values are referred to as costs, since they often entail effort or pain. Third, there are action value (AV) signals that, by integrating the SV and AC, provide an integrated representation of the value of taking the action, once the costs and benefits are taken into account (Rangel and Hare, 2010).

Now think about the comparator process. In a world without noise (a world with no stochasticity in perception or in neural computation), the brain would be able to precisely measure these three variables, and to reliably make the value maximizing decision simply by implementing the following rule: choose left (=Yes) if the reading of the AV signal is positive, and right (=No) otherwise. However, as the literature in perceptual decision making has shown (Gold and Shadlen, 2007; Heekeren *et al.*, 2008), noise is pervasive in these types of computations, in the sense that SVs, ACs and AVs are measured with noise, which makes the simple value maximization rule described before untenable. Instead, a growing body of literature suggests that the brain has dedicated processes to deal with the problems introduced by this noise. In particular, suppose that the instantaneous AV signals are computed with identical and independently distributed Gaussian noise. Then, a general class of processes known as Drift-Diffusion Models (DDM) implement the optimal statistical solution to this problem, which entails a sequential likelihood ratio test. This important class of models are discussed in more detail in Chapters 3 and 19.

Although multiple flavors of these models have been proposed, the following simple and popular version (Ratcliff, 1978; Ratcliff and McKoon, 2008) provides a highly accurate quantitative description of the choice and reaction time curves generated by simple choice

tasks (Basten *et al.*, 2010; Gluth *et al.*, 2012; Krajbich and Rangel, 2011; Krajbich *et al.*, 2010, 2012; Milosavljevic *et al.*, 2010). A simple DDM assumes that a binary choice is made by dynamically integrating the noisy AV signals (Figure 8.1C). This leads to an integrated relative decision value signal that measures the estimated relative value of the left (=Yes) versus the right (=No) choices. The signal starts at zero and at every instant t evolves according to the formula:

$$R_{t+1} = R_t + \theta\,(\mathrm{AV(Yes)} - \mathrm{AV(No)}) + \varepsilon_t, \qquad (8.1)$$

where R_t denotes the level of the signal at instant t (measured from the start of the choice process), θ is a constant that affects the speed of the process, and ε_t denotes an independent and identically distributed error term. The process continues until a pre-specified *barrier* is crossed: the left (=Yes) action is chosen if the upper barrier at $+B$ is crossed first, and the right (=No) action is chosen if the lower barrier at $-B$ is crossed first. If the choice of "No" leads to no consumption, we can set $\mathrm{AV(No)} = 0$ (since both SV and AC are equal to 0).

This model of the comparator has several important features. First, since the integrated relative value signal evolves stochastically, choices and reaction times are inherently noisy, as they are in the data. Second, the model predicts a logistic psychometric choice curve in which the probability of left (=Yes) increases with AV (Yes), and reaction times are decreasing on the same variable. Third, individuals can make mistakes, in the sense of not choosing the best option, but the probability of doing so decreases with the barrier size B, the slope of integration θ, and the strength of the underlying AV signal. In particular, the relative decision value R_t can be thought of as the accumulated evidence in favor of the hypothesis that the left action is better (when $R_t > 0$), or the accumulated evidence in favor of the alternative hypothesis (when $R_t < 0$). The more extreme these values become, the less likely it is that the evidence is incorrect. Finally, the probability of making a mistake can be controlled by changing the amount of noise in the integration process.

The model of simple choice outlined in this chapter also states that the three signals are encoded simultaneously and that the SV and AC only interact when they come together to compute the net action values. After the various value signals are computed, they are integrated by the comparator system until a choice is made. Thus, the duration of the value computations is controlled by the comparator.

It is important to emphasize that there are alternative model specifications of simple choice that, a priori, seem equally plausible. For example, consider a version of the model in which AVs are not computed separately, and instead the SV and ACs are fed additively into the comparator. This alternative model generates identical behavioral predictions provided that the weights of the different signals are appropriately chosen. A strength of the neuroeconomic approach is that it allows for empirical tests of different computational models using neural data: under the first hypothesis we should find units engaged in AV coding and feeding this information to the comparator, whereas in the second version we should not find AV signals, and instead the SV and AC regions should interact directly with the comparator network.

The model also highlights an important distinction between pure SV coding activity and areas that provide representations of multiple kinds of value signals at the same time, often called "multiplexed" signals (Hayden and Platt, 2010; Kennerley *et al.*, 2009). In particular, a "pure SV" unit or region is responsive to the SVs but not to the ACs. In contrast, areas involved in the representation of AVs, or in the dynamic value signals of the comparator, do not entail pure SV coding since they also represent other computations, such as the integration of benefits and costs.

Because of the central role of SVs in neuroeconomics, this chapter focuses on the computation of SVs alone, and not on the computation of ACs, AVs, or how they are integrated and compared. For reviews of AC and AV coding see Chapter 21 of this volume or (Rangel and Hare, 2010; Rushworth *et al.*, 2011; Wallis and Kennerley, 2010). For behavioral and neural evidence related to the drift diffusion model, or DDM, see Chapter 19 and Basten *et al.* (2010), Hare *et al.* (2011b), and Krajbich *et al.* (2010).

METHODOLOGY: HOW TO IDENTIFY STIMULUS VALUE SIGNALS?

In order to take the model of simple choice to the neural data using the tools described in Chapter 4, two additional things are necessary: a methodology to obtain subject specific measures of the SVs computed in every trial and a theory of how the computations described above map to neural activity.

Several procedures are widely used in the field to obtain subject- and stimulus-specific measures of SV. One popular option is to obtain an independent measure of the SV taken either before or after the choice task. This is easily done using liking ratings ("how much would you like to get this good at the end of the experiment?"), or Becker-DeGroot-Marschack (BDM) auctions that provide a monetary and incentive-compatible measure ("how much would you be willing to pay to get this good at the end of the experiment?") of the value of each item (Becker *et al.*, 1964). Both methods can be used to measure the value of virtually any stimulus, provided that the subjects' valuations remain

sufficiently stable throughout the experiment. A disadvantage is that it often requires additional data collection dedicated to obtaining these measurements. Another popular option is to estimate SV from the choice data collected during the experiment itself. This can be done under the maintained hypothesis that individual choice probabilities are generated by something like a logistic choice model over the SVs and ACs (Luce, 1959; McFadden, 2005). If the number of stimuli is small, or if SVs can be described using a simple parametric function of a small number of parameters (e.g., prospect theory; Kahneman and Tversky, 1979; Tversky and Kahneman, 1992), this suffices to estimate the SV of each choice object. The advantage of this method is that it does not require additional data collection. The disadvantage is that sometimes the parameters cannot be estimated with the desired level of precision. For this reason, many groups often use a hybrid of the two procedures (Hare *et al.*, 2009) in which subjects are asked to indicate their choices using a five point scale: Strong No, No, Indifferent, Yes, Strong Yes. This allows subjects to simultaneously indicate their choice and their valuation for the stimulus, as both Strong No and No indicate a negative choice, but with Strong No indicating a lower SV.

The neuroeconomics literature has assumed that SVs and ACs are encoded either in single neurons, or in populations of neurons within a brain region. Under this assumption, the firing rate of such units in every trial, or the activity level of such regions, should be proportional to the subject- and stimulus-specific SV measures obtained using the procedures described above. This prediction can be tested using single unit neurophysiology, blood-oxygenation-level-dependent (BOLD) signal from fMRI, electroencephalography (EEG), or magnetoencephalography (MEG) to look for neurons or brain regions in which the measures of neural activity correlate with the inferred SVs.

A very important point is that although this is the empirical test emphasized in most studies, it is not a sufficient step to conclude that a brain region encodes SVs – a point stressed with regard to any neural variable in Chapter 4. In particular, the following additional tests are also needed to draw such a conclusion.

First, there are pervasive potential confounds that need be ruled out. In most paradigms, SVs are highly correlated with a number of other value-related signals (Figure 8.2A). The SV of a trial is often highly correlated with a prediction error (PE), which measure unexpected changes in present and future rewards

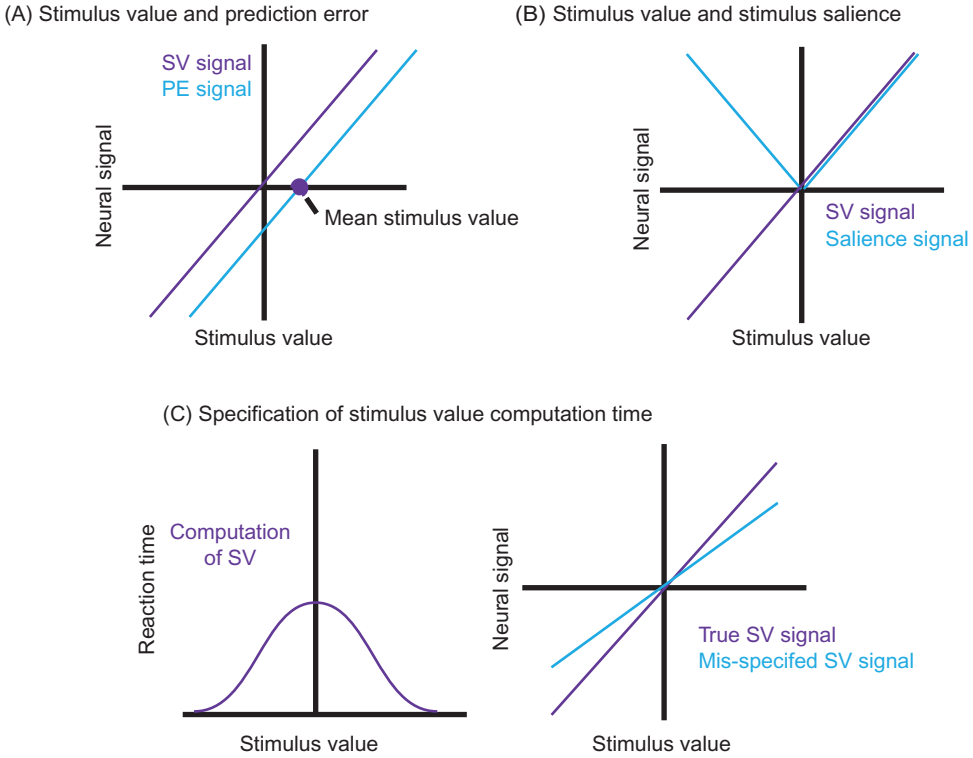

FIGURE 8.2 (A) Stimulus value signals (purple) and prediction errors (blue) can frequently be confounded in a decision-making paradigm. For example, if the decision maker does not know with certainty what their decision will be between, a prediction error can result for "better than average options" or "worse than average options." (B) Salience and stimulus value can also be confounded, if as is shown, rewards only have a positive valence. (C) Reaction time is also important to include when estimating neural responses to stimulus value, with bias depending upon a positive or negative value. See main text for more details.

(Hare *et al*., 2008; McClure *et al*., 2003; O'Doherty *et al*., 2003; Schultz *et al*., 1997). This confound arises from the fact that there will be a PE whenever choice options are revealed. To see why, note that finding out that the choice options in a given trial are better (worse) than average is good news because, once the optimal choice is made, it will lead to better (worse) than average consumption. In fact, in some experimental designs PEs are perfectly correlated with the SVs, even if they are distinct from them under many other conditions. In other paradigms, exposure to the choice stimuli generate direct emotional or hedonic responses (for example, pictures of attractive faces) that are also correlated with, but distinct from the SVs. These confounds need to be identified and systematically ruled out. One approach to addressing this confound is to add forced-choice trials in which the subject is exposed to the same stimuli, but does not make a choice. This works because SV signals should be present during free but not forced choices, whereas direct affective responses to the stimuli (that are unrelated to choice) should be present in both types of trials.

Second, many paradigms confound arousal, motor preparation, and pure attentional processing with SVs (Maunsell, 2004). This potential confound is especially acute in paradigms that use only appetitive or aversive stimuli, but not both. As shown in Figure 8.2B, a good way to eliminate this confound is to combine appetitive and aversive stimuli. Such a paradigm helps because SV signals are monotonically increasing over the entire value range, whereas arousal, motor preparation and attentional signals are U-shaped. Another common term for this second type of signal is *saliency*, which provides a measure of the importance of the stimulus. A powerful and provocative illustration of this problem was provided by a recent study that showed that electromyography measures of activity in neck and jaw muscles, which presumably reflect either motor preparation or arousal, are correlated with SV during a simple choice task (Roesch and Olson, 2003). Thus, in the absence of the controls described here, one would erroneously conclude that these muscles encode SV. This illustrates the critical importance of systematically ruling out these types of confounds.

Third, another source of potential confounds is due to the presence of neurons encoding "multiplexed" value signals (Hayden and Platt, 2010). Neurons encoding pure SV signals should not be responsive to information about ACs, and should be encoded in stimulus space, thus omitting information about the actions required to implement them. This test is important to separate activity related to multiplexed signals (such as a neuron that encodes AV = SV − AC, and thus correlates with SVs) from activity related to pure SV signals (which correlates with SV but not with AC).

Fourth, the model also generates predictions about how SV signals are used in concert with other computations to make a choice. In particular, they predict that SVs should be passed to areas involved in the computation of AVs, the implementation of the comparator process, or both. This implies that areas recruited in SV coding should also exhibit increased functional connectivity with areas involved in computing AVs and in the comparison process at the time of choice. These connectivity tests are important because, under the assumptions of the model, they provide additional evidence in support of the hypothesis that an area encodes SVs that are used to guide choices.

Fifth, SV identification requires correctly understanding the duration of the SV computations (Figure 8.2C). The model predicts that SVs are encoded until a choice is made, and that choice duration is inversely proportional to SV. Many fMRI studies ignore this point and instead model the BOLD responses under the assumption that the valuation process has equal duration for all stimuli. As shown in Figure 8.2C, this biases down the estimates of strength of the neural signals, which can result in a mistaken failure to identify neural responses associated with the computation of SVs. Thus, an absence of a finding – if this issue is not resolved – might correspond to incorrectly concluding a neuron or region does not encode SV.

Sixth, the model of simple choice outlined here assumes that the SV signals causally influence the choices that are made, and none of the tests described above address this component of the theory. The issue of testing for causality of SVs is thus an important yet difficult one. The chapter returns to this issue in a later section.

This section has established that safely concluding that a neuron or brain region encodes a pure SV signal is a hard problem, requiring much thoughtful experimental design and numerous controls. Ideally, every single study would be able to address all of them. Historically, this has not been the case, partly because of the inherent difficulties, and partly because early research in neuroeconomics has sometimes showed weaknesses in these methodological issues. Fortunately, however, the body of data available today, taken as a whole, provides all of the necessary checks and, as described in the next section, has led to a robust set of findings regarding the computation of SVs.

EVIDENCE: STIMULUS VALUE SIGNALS IN BASIC VALUATION TASKS

This section describes key studies and findings regarding the neural basis of SV signals. It focuses

on human fMRI work because, as described in the next section, most existing monkey neurophysiology experiments have used tasks that introduce additional theoretical and methodological complications that make it difficult to draw precise conclusions about the value computations taking place.

The studies described below are based on three different variations of the task depicted in Figure 8.1A. Some studies simply ask subjects to provide a value for each stimuli, either using liking ratings (Grabenhorst *et al.*, 2010; O'Doherty *et al.*, 2003; Plassmann *et al.*, 2008), or incentive compatible bids (Clithero *et al.*, 2009; De Martino *et al.*, 2009; Plassmann *et al.*, 2007). In either case, the logic behind the tasks is to induce subjects to activate the SV circuitry without necessarily activating the rest of the choice circuitry. (Although there is an unresolved issue of whether these tasks fully eliminate the computations associated with the comparator process since such tasks still require the brain to select which button to press to report a bid). Other studies have used a version of the task in which every trial subjects choose between the stimulus shown and "getting nothing," and in which the actions required to implement the choices are button presses with negligible and identical costs. In this case, ACs are approximately zero, AVs are approximately equal to SVs, and SVs are the sole inputs into the comparator process. Finally, a popular class of tasks involves choices between a reference stimulus that is held constant for the entire experiment, and another option that changes every trial. So, again, the choice task is binary and includes a constant option (like "get nothing"), but now the constant option has some nonzero value. Typically, only the option that changes on each trial is displayed (subjects will be shown the reference option at the start of the experiment and/or intermittently during the experiment). Both of the choices have negligible and identical action costs. This design – which holds the SV of one of the choices constant – is useful because the variation in neural activity in an area encoding SVs is driven solely by the varying option. As a result, it is possible to look for SV signals simply by looking for correlates with the varying option.

An initial wave of studies used the methodology described above to identify areas in which neural responses at the time of choice, as measured by BOLD fMRI, correlates with measured SVs. We highlight three studies that illustrate the use of the three different types of paradigms. In Plassmann and colleagues (2007), depicted in Figure 8.3, hungry subjects were shown a picture of a familiar food snack on every trial and had to decide how much to bid for the right to eat that snack food at the end of the experiment. The bids provide a behavioral measure of the SVs on every trial, since they were elicited using the incentive compatible BDM mechanism. The study found that responses in ventromedial prefrontal cortex (vmPFC) and right dorsal lateral prefrontal cortex (dlPFC) correlated with the bids, but no other neural correlates of SVs were found. The paper also included a control to rule out the concern that these signals might reflect affective responses to the foods (e.g., arousal) that are correlated but distinct from SVs. In Kable and Glimcher (2007), depicted in Figure 8.4, subjects were asked to choose between pairs of monetary rewards to be delivered with different delays, ranging from hours to months. One of the options was a constant reference point involving an immediate payoff. They found that activity in vmPFC, ventral striatum (vSTR), and posterior cingulate cortex (PCC) correlated with the SV of the delayed varying option. In Tom *et al.* (2007), depicted

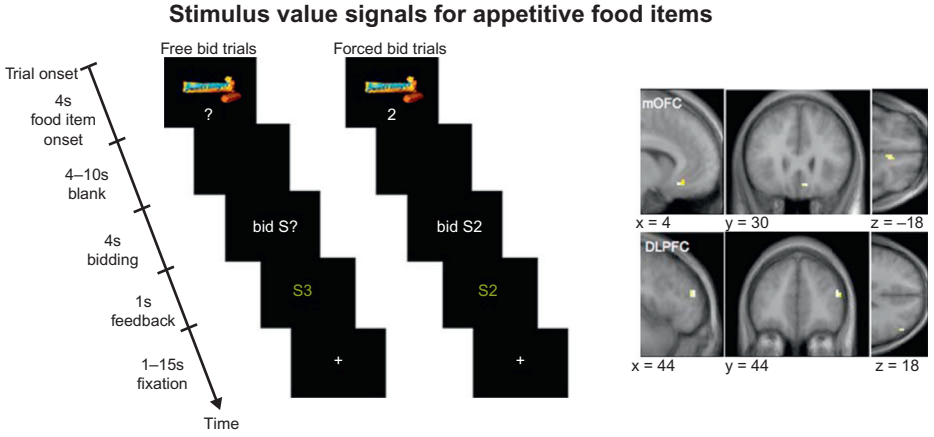

FIGURE 8.3 An fMRI study of willingness-to-pay (WTP). Hungry subjects made bids (either free or forced amounts) on various snack items, which were the only available options to eat after the experiment. The subjective value – measured as WTP – correlated with increased activity in both vmPFC (labeled as medial OFC in the paper) and dlPFC. *Figures are from Plassmann et al. (2007).*

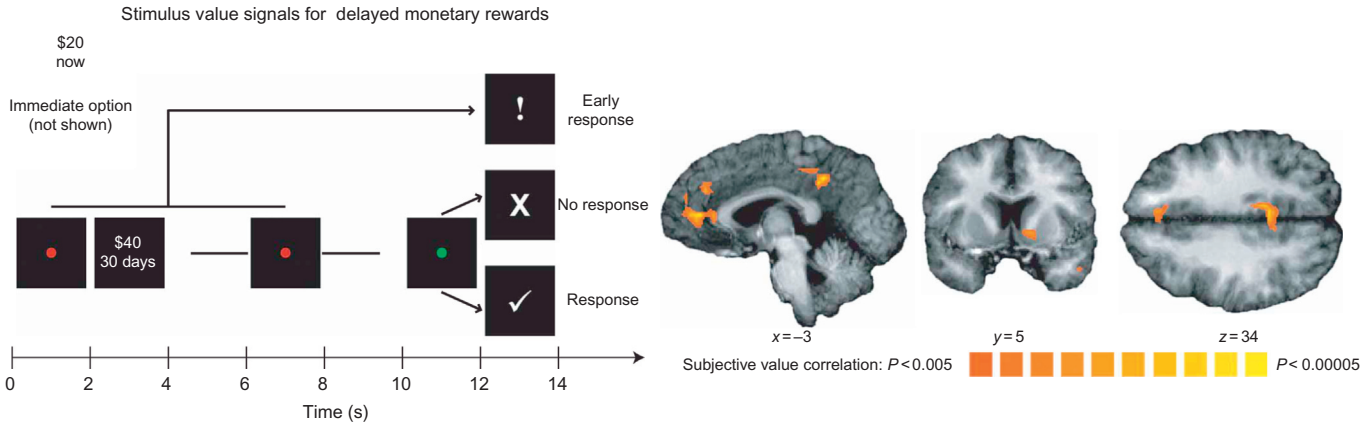

FIGURE 8.4 An fMRI study of delay discounting. Subjects chose between a constant, immediately available amount of money and a larger amount of money available at a future date (left). Areas that correlated with subjective value included vmPFC (sagittal slice), vSTR (coronal slice), and PCC (axial slice). *Figures are from Kable and Glimcher (2007).*

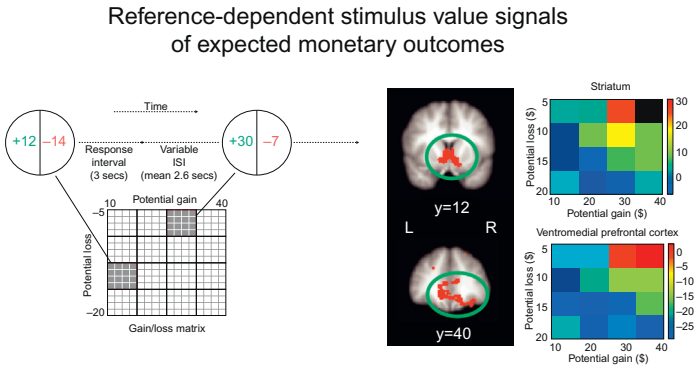

FIGURE 8.5 An fMRI study asked subjects to accept or reject 50/50 gambles of different positive (green) and negative (red) monetary outcomes. In both vSTR (right, top slice) and vmPFC (right, bottom slice), areas that were conjointly significant for parametric responses to gains and to losses, there was evidence for a neural measure of loss aversion. *Data are from Tom et al. (2007).*

in Figure 8.5, subjects were shown 50/50 gambles involving both a potential monetary gain and a potential monetary loss, and were asked to choose between them and a fixed reference payoff of $0. The study found that a similar area of vmPFC and vSTR correlated with the value of the potential gains and losses. Similar results have been found in dozens of follow-up studies (Hare *et al.*, 2010; Knutson *et al.*, 2007; Peters and Buchel, 2009; Prevost *et al.*, 2010; Wu *et al.*, 2011). Together, these studies provide convergent evidence for the hypothesis that the vmPFC is involved in the computation of SV signals during simple choice.

However, as was emphasized in the previous section, further tests are necessary to rule out important confounds, and to test additional properties of the proposed model of simple choice. First, its needs to be ruled out that vmPFC responses might reflect saliency like responses, such as arousal, motor preparation, or attentional modulation. One recent study tested for this confound by showing appetitive and aversive foods, and asking subjects to indicate if they wanted to eat them at the end of the experiment (Litt *et al.*, 2011). A randomly selected decision was implemented. This design made it possible to dissociate SV signals (that increase monotonically with value) from saliency like signals (that have a U-shape with a minimum for neutral items). As shown in Figure 8.6, the study found that activity in vmPFC and PCC was consistent with SV coding, whereas responses in dorsal anterior cingulate cortex (ACC), insula, supplementary motor area (SMA), fusiform gyrus, and precentral gyrus were consistent with saliency coding. The only area that exhibited a combination of SV and saliency coding was the vSTR. In addition, a closely related monkey neurophysiology study found

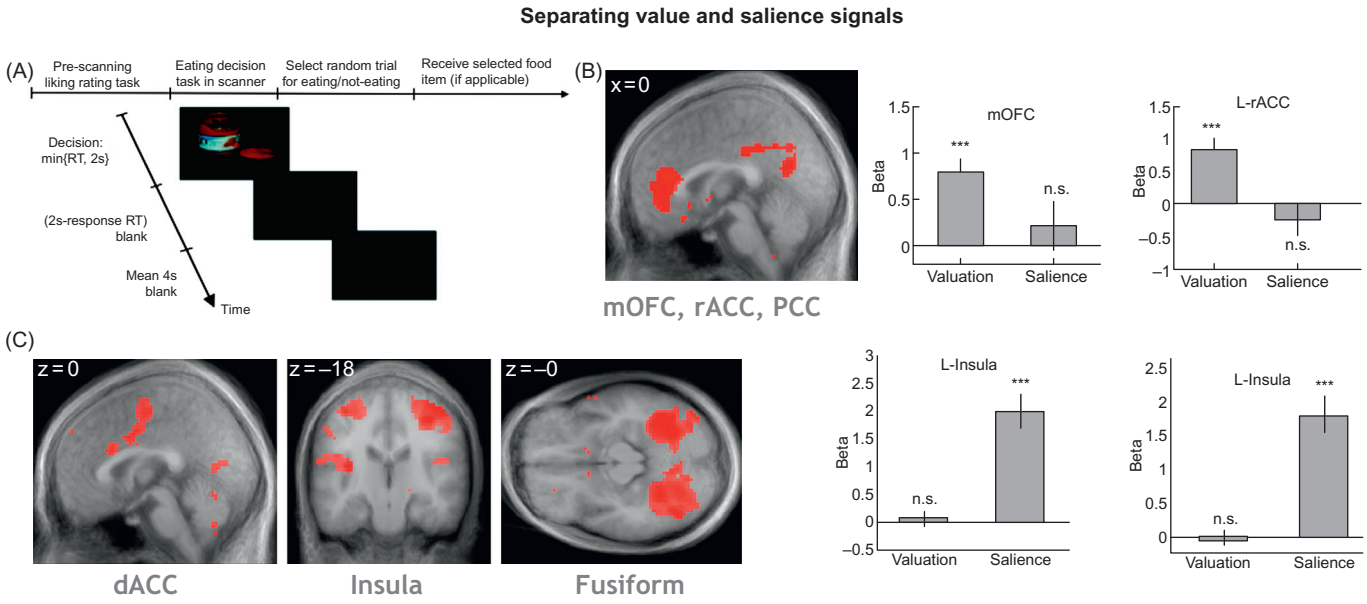

FIGURE 8.6 (A) A simple choice task designed to dissociate stimulus value signals from saliency signals. (B) The study found value-sensitive signals in both medial OFC (mOFC) and the rostral anterior cingulate (rACC), as well as PCC. (C) Saliency correlated significantly with several distinct regions, including dorsal ACC, insular cortex (insula), and bilateral fusiform gyrus. *Images are from Litt* et al. *(2011).*

that neurons in vmPFC were consistent with SV coding, but that activity in the premotor cortex was more consistent with saliency coding (Roesch and Olson, 2004).

Second, it must be determined whether or not the vmPFC responses might encode highly correlated PE signals, instead of the SV signals. One study addressed this problem by combining a food purchasing task with a passive monetary lottery (Hare *et al.*, 2008). As shown in Figure 8.7, at the beginning of each trial subjects were shown a food and a purchase price, and had to decide whether or not they wanted to purchase it. At that time they were also shown the outcome of an exogenous monetary lottery that paid a different random amount every trial. As a result, the PE signal at the time of choice was proportional to the value of the trial, given by the value of the food minus its price plus the outcome of the lottery for trials in which the item is bought, and to the outcome of the lottery for trials in which it is not. Since the food and lottery parameters were selected independently, this made it possible to dissociate regions encoding PEs from those encoding SVs. The study found that SVs were reflected in vmPFC responses, whereas PEs where reflected in the activity of the vSTR. A striking pattern in this literature is that some studies find that vSTR responses correlate with SVs, but many others do not. This is puzzling because the PE confound is present in virtually every choice task. Further work is necessary to understand the source of this important inconsistency.

Third, studies have also tested if the vmPFC responses are modulated by action-related information, which would be inconsistent with the encoding of a pure SV signal. A recent fMRI study created a paradigm in which subjects were shown the choice options before being shown the movements required to obtain them (Wunderlich *et al.*, 2010). This allowed subjects to choose one of the stimuli without knowing which actions they would have to take to implement that choice. The study found evidence for SV coding in the vmPFC before the action contingencies were provided, which suggests that action information is not required for these representations. See Glascher *et al.* (2009) for additional corroborating evidence, although it should be noted that this conclusion is not universally accepted in the neuroeconomics field.

Fourth, another important property of a SV signal is that it is a precursor of choice, and thus it should not depend on the outcome of the decision process. Consistent with this, Hare *et al.* (2011a) Lim *et al.* (2011) have shown that the sign and strength of the

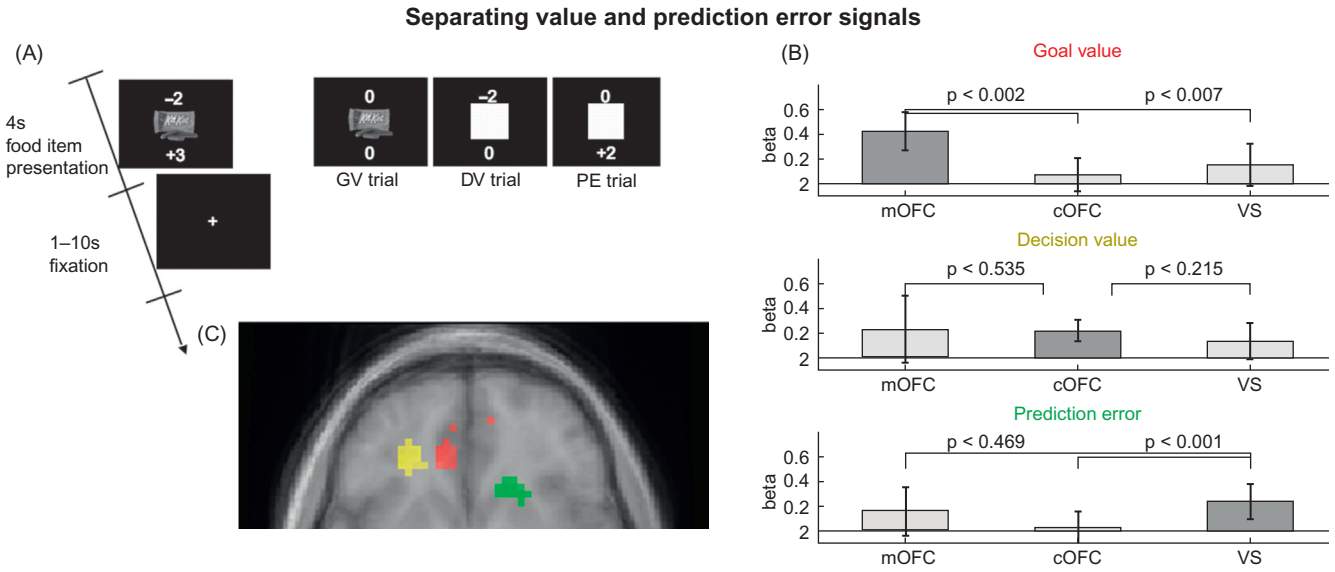

FIGURE 8.7 An fMRI study of different value computations. (A) At the beginning of each trials, subjects were shown a food and a purchase price and then decided whether or not to purchase. Trials dissociated *goal value* (GV), *decision value* (DV), and *prediction errors* (PE). (B and C) We consider both GV and DV to be stimulus values. The study found that SV where reflected in vmPFC responses (red and yellow), whereas PE where reflected in the activity of the vSTR (green). *Data are from Hare* et al. *(2008).*

vmPFC responses at the time of choice depend on the stimuli being evaluated, but not on which of them is chosen.

Fifth, according to our model, SVs are used as inputs to the comparison process (either directly, or indirectly through the computation of AVs, as shown in Figure 8.1C). As a result, one would expect that areas involved in SV computations would exhibit increased functional connectivity with the network involved in the comparison process at the time of making decisions. Two studies found several pieces of key evidence consistent with this (Basten *et al.*, 2010; Hare *et al.*, 2011b). In particular, Hare *et al.* (2011b) argues that a brain area involved in implementing the comparison process must exhibit the following properties: (i) its activity in each trial at the time of choice should correlate with the total level of activity predicted by the a neural implementation of the best fitting DDM of the task; (ii) it should receive as an input signals from the area of vmPFC involved in SV computation; and (iii) it should modulate activity in the motor cortex in a way that is consistent with implementing the choice. The study found that activity in dorsomedial prefrontal cortex (dmPFC) and the bilateral intraparietal sulcus (IPS) satisfy the three required properties.

Additional corroborating evidence can be found in the neurophysiology literature. For example, neurons in dmPFC have been shown to reflect several different decision variables (Kennerley *et al.*, 2009, 2011), making this region ideally qualified to compare the SVs and ACs of different options and select the best course of action. For further details on the computation and comparison of AV, please refer to Chapter 22.

Jointly, the results described in this section provide strong evidence in support of the hypothesis that vmPFC responses at the time of making a simple choice reflect the computation of a SV that is passed (either directly or indirectly through the computation of action values, as in Figure 8.1C) to a comparator system, implemented in areas such as dmPFC and IPS, in order to guide choices.

A significant amount of effort in the field has been devoted to investigating if these key findings are robust to different specifications of the choice task, and if the same region of vmPFC encodes the value of different types of stimuli. Although much work remains to be done, the evidence so far suggests that the findings are quite robust. Consider a handful of examples. One study asked individuals to make choices between a constant reference item and three different types of goods: Caltech bookstore paraphernalia, foods, and monetary lotteries (Chib *et al.*, 2009). The data revealed that the same vmPFC region identified above correlated with the SVs of the three types of objects (Figure 8.8). Futhermore, the location of the SV signals were the same regardless of the type of good (food, paraphernalia or money) used as the constant reference option. Thus, the finding stands even when subjects are not forced to make comparisons to a monetary scale. Further evidence for the stability of the vmPFC value signal across stimulus modalities is provided by Levy and Glimcher (2011). Several studies have also shown

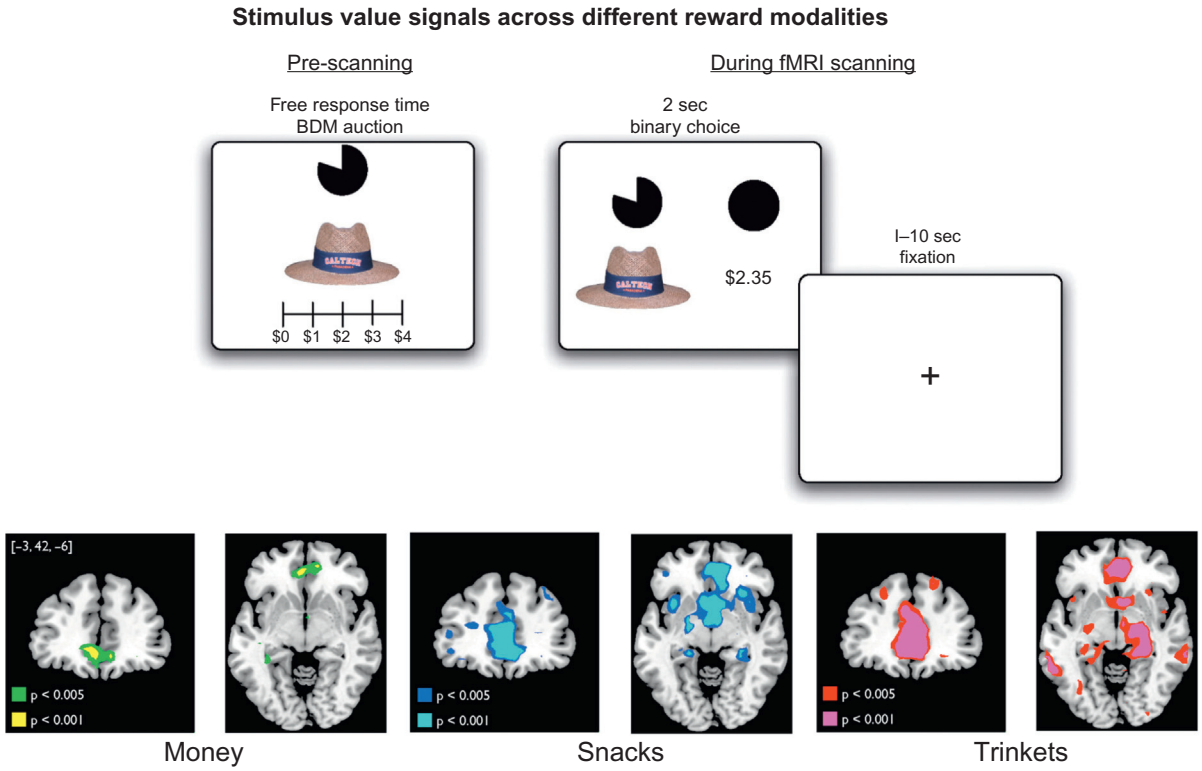

FIGURE 8.8 An fMRI study of choice across several reward modalities. Subjects were asked to make choices between a constant reference item and three different types of goods: Caltech bookstore paraphernalia, foods, and monetary lotteries (top). Importantly, vmPFC identified correlated with the SVs of the three types of objects (bottom), and the location of the SV signals were the same regardless of the type of good (food, paraphernalia or money) used as the constant reference option. *Data are from Chib* et al. *(2009).*

that the vmPFC correlates with SVs during social decision making (Hare *et al.*, 2010; Lin *et al.*, 2012). Studies have also shown that vmPFC encodes the overall SV of the choice options, even in circumstances when they have to be computed by integrating complex information (Figure 8.9), such as different reward probabilities (Kahnt *et al.*, 2011; Philiastides *et al.*, 2010). The SV representations in vmPFC have even been shown to be present when individuals are not explicitly making choices and are instead "passively" exposed to the stimuli (Lebreton *et al.*, 2009), sometimes associated with the phrase "automatic valuation" (Figure 8.10). In fact, the signals are robust enough to be able to predict subsequent choices (Levy *et al.*, 2011; Smith *et al.*, 2010; Tusche *et al.*, 2010).

Several papers have also investigated if the same area of vmPFC encodes the SV of appetitive and aversive items using a common scale. This question is motivated by the fact that many psychological theories assume that choices among appetitive items, sometimes called approach choice, and choices among aversive items, sometimes called avoidance choice, involve separate systems (Larsen *et al.*, 2004). Under this theory, the approach system encodes how good a stimulus is, and thus correlates positively with SVs. In contrast, the aversive system encodes how bad a stimulus is, and thus correlates negatively with SVs. An fMRI study compared the areas involved in computing the value of appetitive and aversive food items using a bidding task, and found that common areas of vmPFC correlated positively with the SV of the items, regardless of their valence (Plassmann *et al.*, 2010). Related studies using multi-attribute monetary stimuli involving gains and losses suggest that both of them are processed and integrated in the same area of vmPFC (Basten *et al.*, 2010; Park *et al.*, 2011; Tom *et al.*, 2007). These studies are important because they show that, at least in the case of simple choice, the same area of the brain seems to encode the decision value for both types of choices, thus providing evidence against the hypothesis that there are separate appetitive and aversive valuation systems in goal-directed choice.

Finally, a number of studies also investigated the timing with which SV signals appear in vmPFC. Behaviorally, one study found that individuals can make value maximizing choices with above chance reliability in about 300 milliseconds (ms), which implies that SVs must be computed faster than this

(Milosavljevic *et al.*, 2011). An EEG and source reconstruction to identify the area of vmPFC associated with the computation of SVs, and found that a very similar area to the one identified in the fMRI studies exhibited activity proportional to the SVs about 400 ms into the decision process (Harris *et al.*, 2011). Similarly, another study employed MEG to investigate related questions and find reliable SV in vmPFC in a similar time scale (Hunt *et al.*, 2012). Finally, another fMRI study investigated the duration of the SV signals computed while subjects made Yes/No food choices at different exogenously imposed speeds (Sokol-Hessner *et al.*, 2012). The results suggest that the SV computations in vmPFC and dlPFC were slower in slower trials, even though the additional computation time had little impact on the quality of the choices.

Although this chapter has demonstrated that SVs appear to reliably be encoded in vmPFC, how precise is the localization in vmPFC? A careful look at the studies of SV highlighted in this chapter shows the area of vmPFC identified in all of these humans studies is fairly consistent (Levy and Glimcher, 2012; Roy *et al.*, 2012). Furthermore, although the evidence so far is only correlational, the stringent nature of all the additional tests described above provides increased support to this hypothesis. The limited existing evidence on causality, which will be discussed in a later section, is also supportive of this conclusion.

These results suggest an anatomical and functional dissociation between the vmPFC, which is involved in computing stimulus values, and areas of dmPFC and IPS which are involved in implementing the comparison process. As depicted in Figure 8.11A, in humans vmPFC includes regions of medial orbitofrontal cortex (OFC, areas 11 & 14), as well and part of ventral medial cortex (area 10), but does not include central or lateral OFC (areas 13 and 12/47 respectively) (O'Doherty, 2011; Wallis, 2012). Interestingly, vmPFC is reciprocally connected with many areas involved in

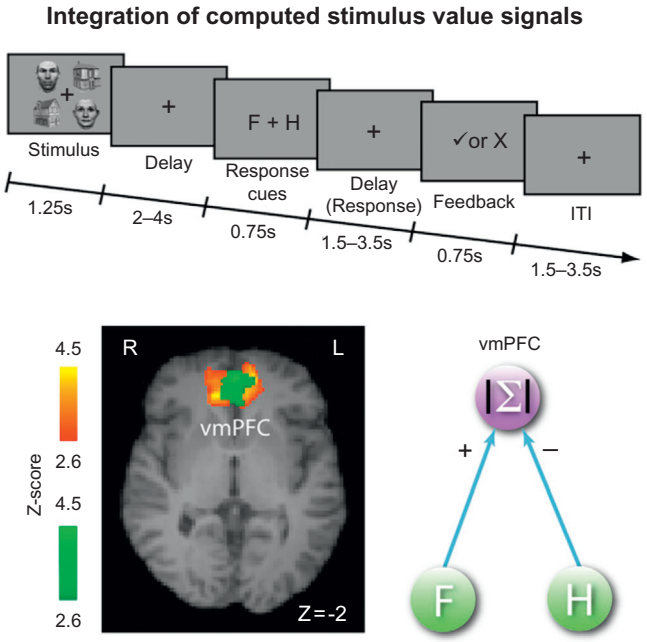

FIGURE 8.9 An fMRI study of how the brain integrates complex information. On each trial (top), subjects viewed four images of faces and houses, and had to choose whether or not a house or a face would provide a reward. All stimuli represented probabilistic monetary rewards. Only vmPFC showed a signal (bottom) that reflected the combination of evidence for face (F) and house (H). *Data are from Philiastides* et al. *(2010).*

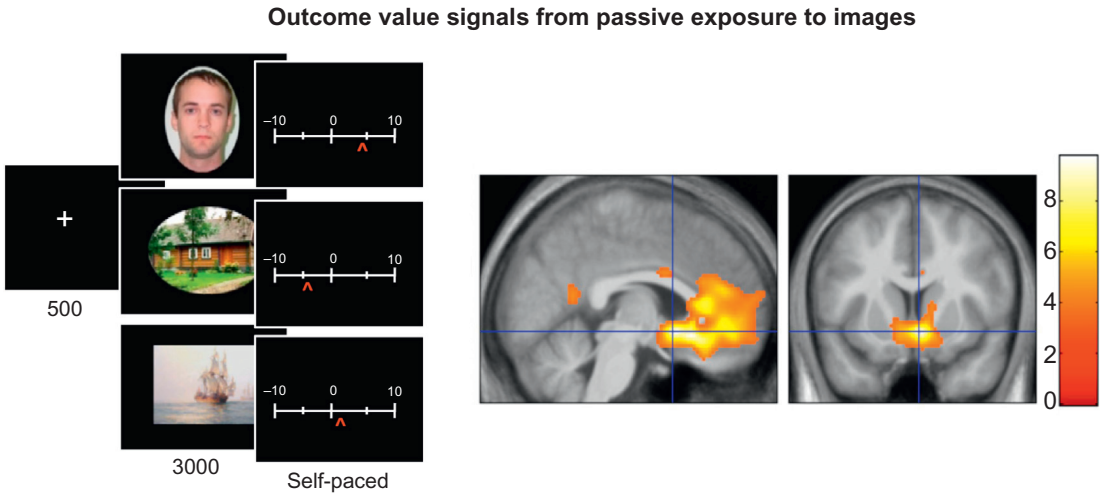

FIGURE 8.10 Participants in an fMRI experiment provided pleasantness ratings for a range of different stimuli including faces, houses, and paintings, and at the end of the experiment indicated preferences between pairs of images. This value signal – a pleasantness rating – correlated with both vmPFC (sagittal slice) and vSTR (coronal slice). *Data are from Lebreton* et al. *(2009).*

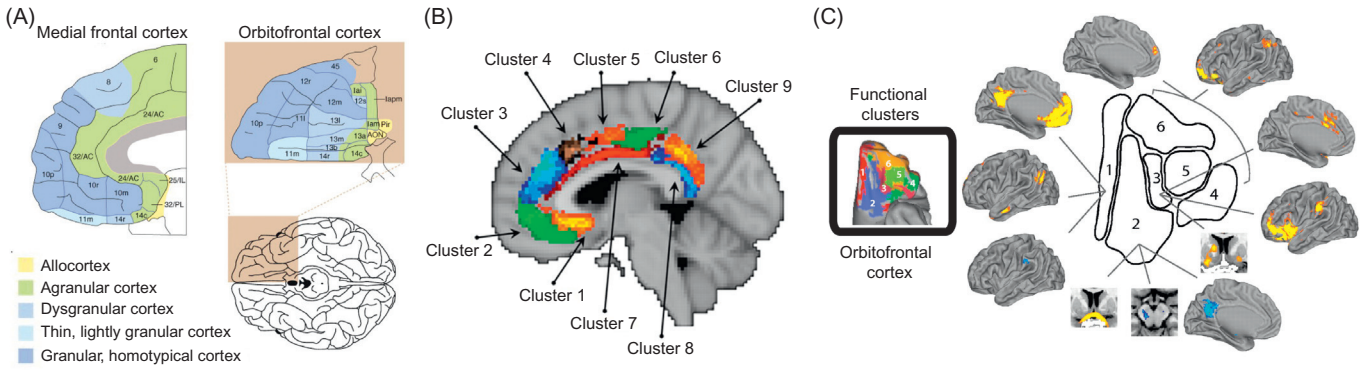

FIGURE 8.11 (A) Anatomy of the human frontal cortex. These archotectonic maps are included to demonstrate the diversity and significant variability in the structure of neighboring regions in human frontal cortex. *Images are from Wise (2008)*, and a similar figure appears in *Wallis (2012)*. (B) A recent study completed a parcellation of human cingulate cortex and medial frontal cortex by using diffusion-weighted magnetic resonance imaging and probabilistic tractography, demonstrating distinct connectivity within much of human frontal cortex. Importantly, cluster 2 (green) demonstrated strong correspondence to a large literature of reward studies. *Data are from Beckmann et al. (2009)*, and see *Rushworth et al. (2011) for additional discussion*. (C) Another recent study used resting-state fMRI data to parcellate OFC. Their analysis found six clusters (inset) with distinct functional connecitivity profiles. Positive connectivity (yellow) was exhibited in all clusters, and negative connectivity was found in some (blue). Note strong connectivity with much of prefrontal cortex, as well as PCC and parts of the striatum. *Images are from Kahnt et al. (2012)*.

affect and cognition, such as hippocampus, amygdala, hypothalamus, striatum, and other parts of prefrontal cortex (see Chapter 12), but is weakly connected with motor areas (Carmichael and Price, 1995; Ongur and Price, 2000). This puts it in a good position to be able to compute SVs, but not to influence decisions directly. In contrast, the dmPFC (sometimes similar regions are labeled as areas of dorsal ACC) is heavily inter- connected with both supplementary motor areas and areas of vmPFC thought to be involved in valuation, but not with sensory areas (Beckmann *et al.*, 2009; Picard and Strick, 2001). A recent parcellation of the entire cingulate cortex (Beckmann *et al.*, 2009) found distinct connectivity for regions discussed in this chapter with respect to SV, primarily clusters 1 and 2, compared with other regions potentially involved in AV, namely clusters 3 through 5 (Figure 8.11B). Another study also completed a functional parcellation of orbitofrontal cortex (OFC), which also includes regions commonly labeled as vmPFC in studies of SV (Kahnt *et al.*, 2012). This analysis of fMRI data indicated distinct connectivity to regions discussed in this chapter, including IPS, ACC, and PCC (Figure 8.11C).

COMPLICATION: ATTENTION MODULATES THE COMPUTATION AND COMPARISON OF STIMULUS VALUES

Although the model and choice tasks described above have been widely used, they do not encompass many simple choice situations of interest. As an example, consider the following situation: choose between a food shown in the left visual field by pressing a button with the left hand, and another food shown in the right visual field by pressing another button with the right hand. This simple example does not correspond to any of the previous studies for a simple reason: both options are allowed to vary every period, so that there is no constant reference option.

Moving to this type of choice environment introduces two important complications. First, suppose that there is relative SV coding (in the sense that the SV of every item is encoded as the difference between its value and that of a reference point, say $SV_{option} - SV_{reference}$), as it seems to be the case from the behavioral (Ericson and Fuster, 2011; Kahneman and Tversky, 1979) and neural data (De Martino *et al.*, 2009). Then, it is not obvious which of the two options should serve as the reference point from which relative values are computed, since both of them are changing every period. Second, attention is likely to fluctuate among the different items being evaluated during the course of the decision, and this might affect the SV computations. Note that this is not a theoretical curiosity, but something that needs to be addressed to understand simple choices in the real world, such as how an individual works through all the options at a buffet table.

Figure 8.12 depicts two binary choice tasks that have been repeatedly used in previous studies. In Figure 8.12A, subjects are shown pairs of snack foods, and are free to fixate back-and-forth until they are ready to make a choice by pressing a button (Krajbich *et al.*, 2010). In Figure 8.12B, subjects have to choose between the left and the right options, which are associated with

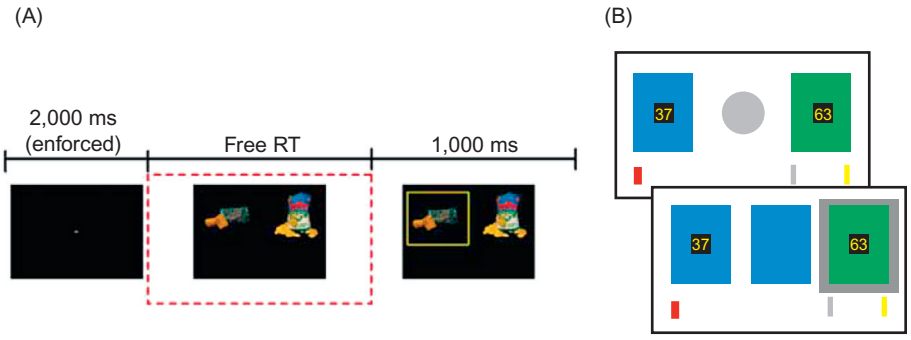

FIGURE 8.12 Two examples of simple choice environments. Subjects choose between (A) two different food items (Krajbich *et al.*, 2010), or (B) two stochastic monetary rewards (Behrens *et al.*, 2007), where feedback for the correct choice (here, blue) is provided after the choice.

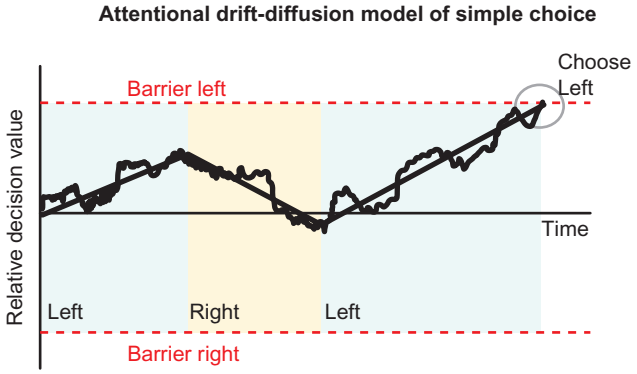

FIGURE 8.13 The attentional drift-diffusion model (aDDM) of choice, *from Krajbich* et al. *(2010)*. The model accounts for attentional shifts that bias the accumulator and comparator introduced in Figure 8.1. In this example, the decision maker ultimately chooses "Left" after the relative subjective value evolves over time, with the slope of accumulation biased towards the option on which the subject is fixated. See text for more details.

a stochastically evolving probability of paying a reward (Behrens *et al.*, 2007; Boorman *et al.*, 2009). The subjects learn the probabilities by trial and error, with the size of the monetary prize for each option being randomly drawn each trial from a known distribution. This last property ensures that subjects cannot make a choice until all of the payoff information is provided (Behrens *et al.*, 2007; Boorman *et al.*, 2009).

Both tasks involve binary choices among options that change every trial, and action costs that are negligible and equal across options. The model in Figure 8.13 extends the model of simple choice to accommodate the additional complications. As before, it assumes that SVs and ACs are computed separately, that they are integrated into a net AV signal, that the AV signal is passed to the comparator to guide the choice process, that the values are computed from the time the options are presented to the time a choice is made, and that value computations are made using a relative subjective value (RSV) code. The key difference is in how the reference points are selected. The model now assumes that at any point in time, SVs and ACs encode the value/cost of the attended option minus the value/cost of the unattended one. Thus, when the subject looks left, the SV signals encode the value of left minus the value of right stimuli, and the opposite is true when he looks right. This implies that visual attention at any particular instant determines the identity of the reference point. One additional assumption is that the SV value of the attended item might be weighted more heavily, so that the relative SV signal is given by:

$$RSV_t = \alpha\, SV(\text{attended item}_t) - SV(\text{unattended item}_t). \tag{8.2}$$

The parameter α measures the strength of the attentional bias, with $\alpha = 1$ denoting the case of no bias.

In the types of tasks studied here, the ACs are identical and negligible, and as a result they can be assumed to be zero. This implies that AVs are directly proportional to SVs, and that the same attention-based relative value code applies there. If this where not the case, the AC signals would be computed using an analogous attentionaly modulated relative code.

The model discussed in this section is known as the attentional DDM (aDDM) (Krajbich and Rangel, 2011; Krajbich *et al.*, 2010, 2012), and it assumes that the comparator process is described by an extension of the DDM. As depicted in Figure 8.13, the model is similar to the basic DDM: it takes the AVs as inputs and integrates dynamically subject to some Gaussian noise until the accumulated evidence for one of the two responses becomes strong enough to cross the pre-specified barriers. The key difference is that the accumulator signal inherits the attentional modulation properties of the SVs and AV signals. This implies that the integrated relative value signal in favor of choosing the left option over the right option evolves according to:

$$\begin{aligned} R_{t+1} = R_t + \alpha\, SV(\text{attended item}_t) \\ - SV(\text{unattended item}_t) + \varepsilon_t, \end{aligned} \tag{8.3}$$

All other elements of the model remain unchanged (refer to Figure 8.1), and methods for identifying the

other model parameters outlined here and in other chapters still apply. As in the DDM, the ε_t term reflects independent and identically distributed Gaussian noise in the integration process.

The model has several novel properties, in addition to those generated by a more standard DDM. First, it makes strong quantitative predictions about the correlation between attention, choices, and reaction times. These predictions can be tested by combining eye-tracking (which provides an instantaneous measure of visual attention in the form of the identity of the stimulus being fixated), choice and reaction time data. For example, it predicts sizable choice biases when $\alpha > 1$: options that were fixated on more, due to random fluctuations in attention, were more likely to be chosen. Using these methods, an eye-tracking study carried out a systematic test of the extent to which the aDDM model can explain these types of patterns, and found that it is able to account for them with high quantitative accuracy (Krajbich *et al.*, 2010). Second, it predicts that experimenter induced changes in attention (for example, through marketing manipulations) should bias choices in favor of the most attended option when its value is positive, but it should have the opposite effect when the value is negative. Consistent with this prediction, several studies have found that it is possible to bias choices through these types of manipuations (Armel *et al.*, 2008; Milosavljevic *et al.*, 2010; Shimojo *et al.*, 2003). Third, it predicts that if the fixation process is independent of the value of the stimuli (so that, for example, higher value items are not fixated on earlier or longer), and there is an attentional bias, then there will be a bias towards fixating on the last option that increases with computation time. The data in the paper first outlining the aDDM (Krajbich *et al.*, 2010) exhibits both of these patterns.

This last point is critical for understanding the neural properties of the SV signals that one would expect to find with techniques like fMRI, that have limited temporal resolution. The model predicts that *in the absence of an attentional bias* (i.e., $\alpha = 1$ in the aDDM model), the average value SV signal in vmPFC over the course of a decision trial should be zero. In this case it would not be possible to identify the underlying SV signals using fMRI. In contrast, if there is an attentional bias (i.e., $\alpha < 1$), and visual attention is not measured and controlled for (as is the case in most studies), the model predicts that the measured SV signal would reflect the underlying attentional bias for the chosen item. In this case, activity in a SV coding area would correlate with the SV of the chosen item minus the SV of the unchosen item. Since this has been a source of confusion in the literature, it is important to emphasize that fMRI measures of the SV signals take this form not because they reflect the outcome of the choice process (as has been argued by Hunt *et al.*, 2012; Jocham *et al.*, 2012), or because they actually encode the value of the chosen and unchosen items, but as a consequence of the properties of the underlying data generating process, and of the limitations of measuring neural signals with fMRI (which have poor temporal resolution, and thus average activity across fixations).

These limitations point to the value of complementing or combining fMRI with methods, such as EEG and MEG, that have better temporal resolution. In the presence of an attentional bias, and as long as attention is not measured and controlled, the model predicts that the SV signal in vmPFC should reflect both the left and right SVs early on, when the attentional bias towards the chosen item is low, and gradually switch to reflect the difference in value between the chosen and the unchosen items as the trial progresses. As long as the source of the SV signals can be reliably localized using these methods (a topic of some controversy, but there have been some efforts to localize such signals; Harris *et al.*, 2011; Hunt *et al.*, 2012), these temporal properties of the signal can be tested using the high temporal resolution measurements provided by EEG or MEG.

One fMRI study carried out a critical test of the role of visual attention in the computation of SV signals. They asked subjects to perform the binary food choice task in Figure 8.14A inside the scanner with two important twists (Lim *et al.*, 2011). First, they exogenously and randomly manipulated the duration and location of fixations. Second, in order to deal with the limited temporal resolution of fMRI, the choice process was slowed down: fixation duration ranged from 1 to 4 seconds, and each item was seen twice before a choice could be made. Consistent with the model, they found that the activity in the same areas of vmPFC discussed before correlated with an attentionally modulated relative code (Figure 8.14A, bottom). The same was true for the vSTR.

A recent MEG study (Hunt *et al.*, 2012) studied the evolution of the vmPFC responses during the course of a binary choice, but did not control for visual attention. Also consistent with the predictions of the model, they found that activity in this area gradually switched from reflecting the sum of the SVs to the difference between the value of the chosen and unchosen options.

Several fMRI studies have looked at the value signals encoded in various types of binary choices. For example, the authors of one fMRI study investigated the nature of value coding in the task shown in Figure 8.14B (Boorman *et al.*, 2009). As predicted by the model describing the role of attention in the computation of SV signals, the study found that vmPFC responses at the time of choice correlated with the value difference between the chosen and unchosen items. Similar results have also been found in other

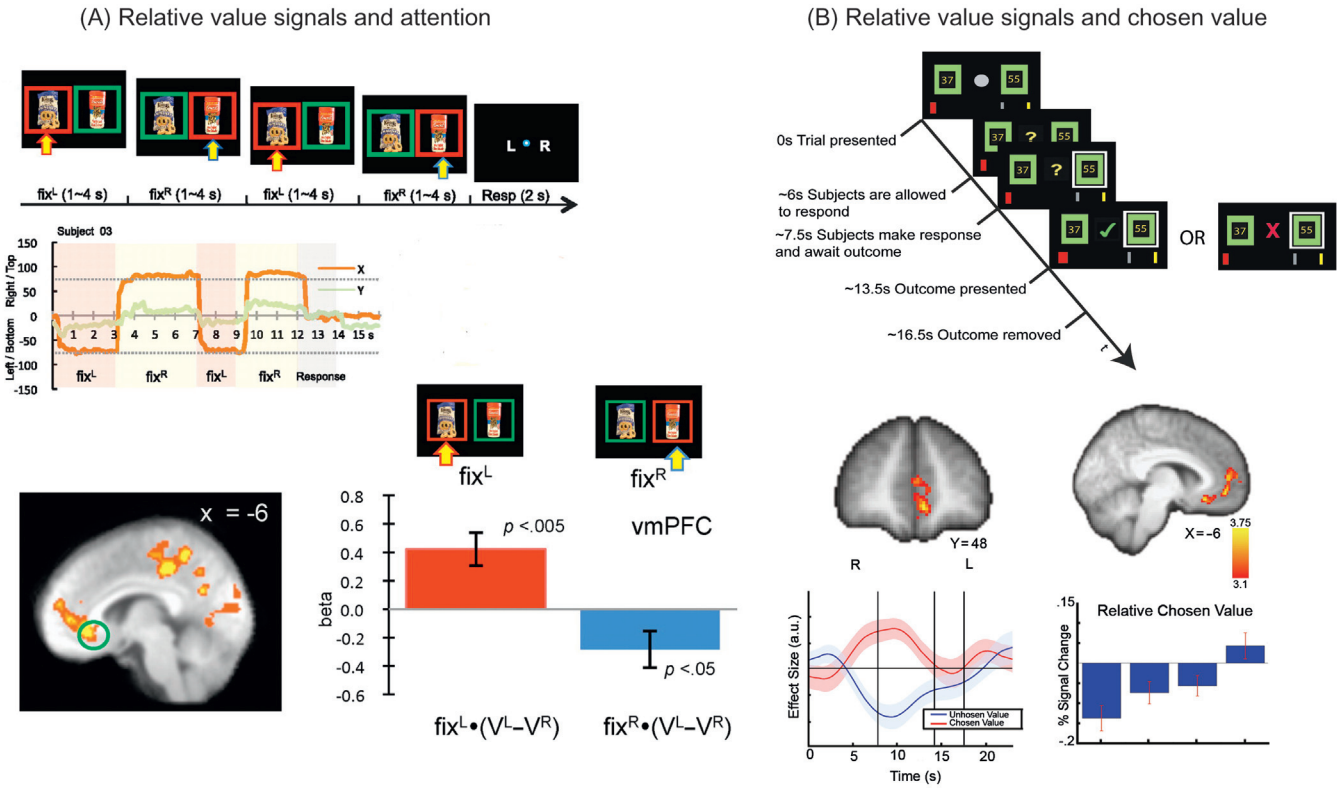

FIGURE 8.14 Implications for chosen value signals with and without accounting for attention. (A) An fMRI study asked subjects to perform the binary food choice task that exogenously and randomly manipulated the duration and location of fixations (yellow arrows illustrate target positions). The study found vmPFC correlated with an attentionally modulated relative value (bottom), meaning the same relative value (left minus right) was greater when subjects fixated left (red) than when they fixated right (blue). *Data are from Lim et al. (2011).* (B) In an fMRI study with a task similar to the one shown in Figure 8.12B, subjects chose between two stochastic monetary rewards (top). Time courses reveal a positive correlation with the chosen reward and a negative correlation with the unchosen reward in vmPFC. Further, the relative chosen value (chosen minus unchosen) was encoded in vmPFC. *Data are from Boorman et al. (2009).*

fMRI studies comparing SV signals for chosen and unchosen options (FitzGerald *et al.*, 2009; Glascher *et al.*, 2009; Talmi *et al.*, 2009).

A reconsideration of some recent monkey neurophysiology studies also highlight the importance of controlling for attention. In particular, there are a large number of neurophysiology papers that have recorded the activity of neurons in the central OFC (cOFC; Brodmann's area 13) during binary decision-making tasks. (Note that most human fMRI studies reference vmPFC for SV signals, whereas many monkey studies report positive results from OFC, a topic of recent discussion; Wallis, 2012.) An extremely influential study is Padoa-Schioppa and Assad (2006), which is depicted in Figure 8.15. Thirsty animals make choices between different amounts of two juices, A and B. The location and amount of the juices changed every trial. Animals indicate their choices through eye-movements when prompted to do so. Using the methods described above, the authors were able to estimate the SVs of all of the options. Their key finding was that during the evaluation period the responses of a sizable fraction of neurons in cOFC correlated with either the SVs of specific juices, or with the value of the chosen option. (The results in the supplementary materials section of that paper suggest that some units might also reflect the value difference between the chosen and unchosen options). This has been widely interpreted as evidence that single units in the OFC encode the value of the chosen option. However, since the study does not control for visual attention, for the same reasons described above, the units reflecting chosen minus unchosen values are also consistent with the computation of attentionally modulated relative value signals. In the case of thirsty and highly trained animals, it may be that the attentional bias is particularly strong, which would further increase the attentional modulation of the chosen option, compared to the unchosen one. Despite this important caveat, the study also provided a separate but criticial insight: the monkey OFC seems

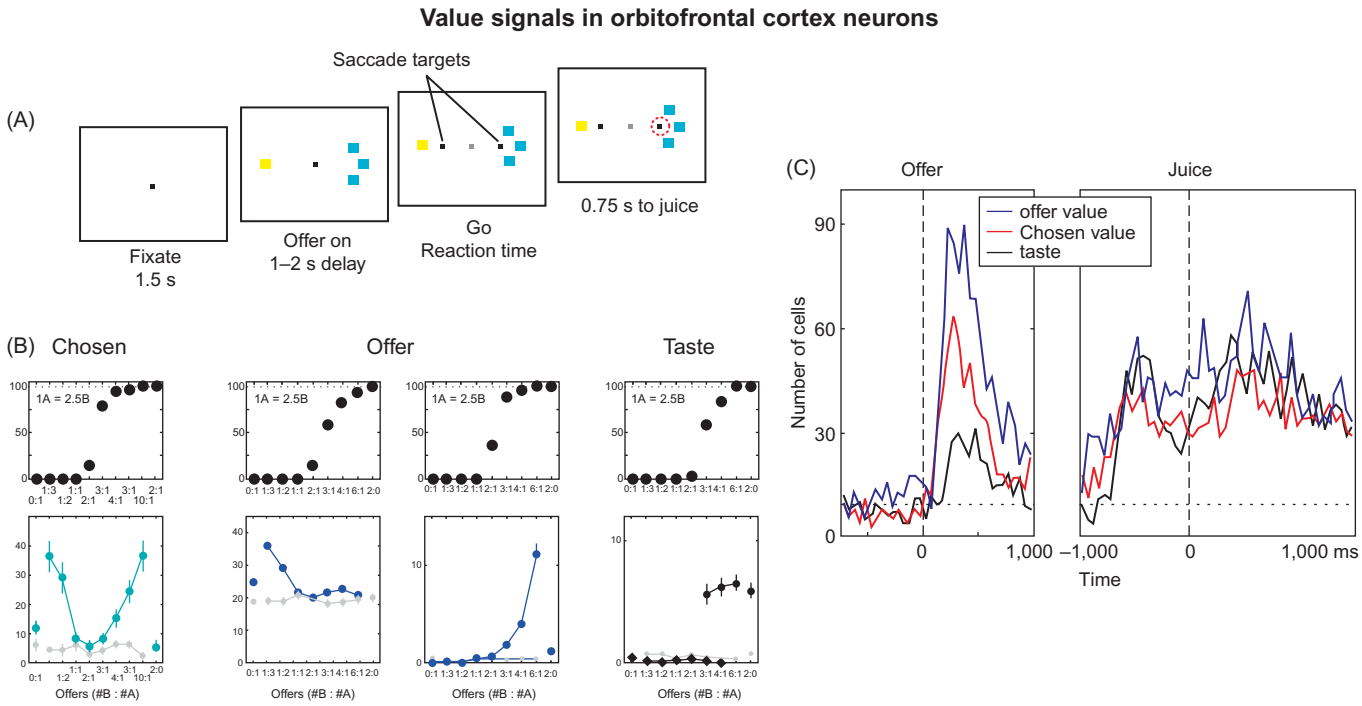

FIGURE 8.15 A neurophysiology study of value signals in OFC. (A) Monkeys chose between different rewards (juices) offered in variable amounts, with different colors paired with different rewards, and the number of squares indicated different magnitudes. (B) Evidence for different neuronal responses to different value signals. A U-shaped relationship for chosen value (left), offer value (middle) that reflects increasing magnitude of juice, and taste (right), where the neuronal response is binary depending upon the chosen juice, not the magnitude. (C) Time courses for the different value signals in OFC, indicating that soon after an offer, some OFC neurons encode the offer value (the SV of one juice or the other), some encode chosen value (but see the main text for discussion of attentional effects), and some encode taste. *Data are from Padoa-Schioppa and Assad (2006).*

to contain an equal proportion of neurons involved in absolute and relative coding. This observation, which has also been replicated (Kobayashi *et al.*, 2010), is important because it suggests that the OFC might first compute the absolute value of the stimuli and then use it to compute a relative and attentionally modulated representation to be passed to the comparator.

Another important and related study is depicted in Figure 8.16 (Kennerley *et al.*, 2011). Thirsty animals made choices between pairs of stimuli that were associated with different amounts of juice delivered with various probabilities, as well as different amounts of required effort (in the form of different numbers of lever presses). Importantly, the lever presses were not part of the choice process, and in fact were "paid" by the monkey at a separate time, thus representing a negative attribute of the stimuli, and not an action cost. Another important feature of their experiment is that in any given trial the stimuli only differed in one of the dimensions, and that to make choices non-trivial items with adjacent values were always paired against each other. This last feature is important because it makes it impossible to distinguish between correlations with SVs (which reflect the value of stimuli independently of the choice made) and chosen values (which reflect the value of the chosen option). A key finding of the study is that units in cOFC (area 13) were more likely to be consistent with the encoding of SV signals. Since the authors did not control for visual attention, the same issues regarding the interpretation of chosen value signals apply here.

An important limitation of the model outlined here is that it does not provide an explanation of what drives the attentional process. One natural hypothesis is that the fixation process is driven in part by the underlying values of the stimuli. However, the data from tests of the aDDM (Krajbich and Rangel, 2011; Krajbich *et al.*, 2010, 2012) suggest that this is not the case: the fixation process exhibits spatial biases (e.g., first fixation to the left item are more likely), but is uncorrelated with independently taken measures of the SVs. A more subtle version of this hypothesis is that at any point in time, attention is modulated by the current representation of the raw and integrated signals, such as those present in vmPFC and dmPFC. Testing this theory is difficult because it requires instantaneous measures of these signals, but is a critical open question for future research.

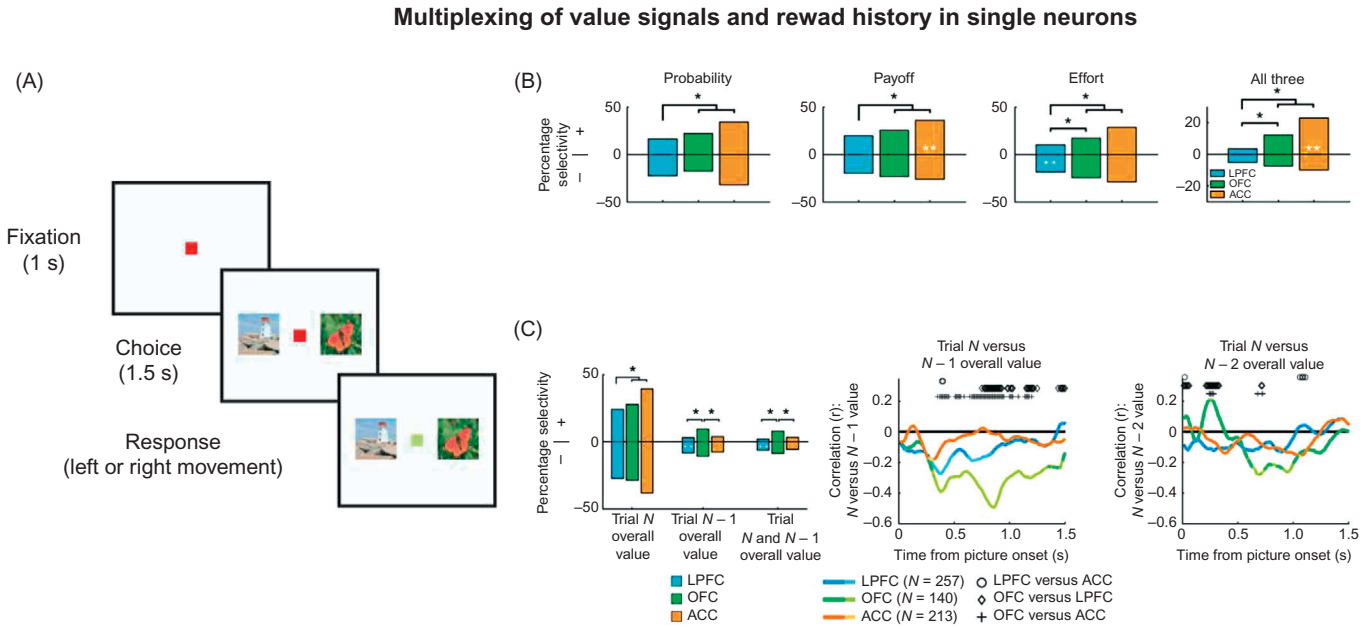

FIGURE 8.16 A neurophysiology study of value signals in three different regions: lateral prefrontal cortex (lPFC, blue), OFC (green), and ACC (yellow). (A) In the task, monkeys made a choice between two stimuli. There were six sets of pictures, each associated with a specific outcome. The amount of reward (juice) and the probability of receiving a reward, as well the amount of effort required varied across images. Monkeys indicate choices with an eye movement. (B) The bar plots show the prevalence of neurons encoding choice value with a positive or negative regression coefficient in lPFC, OFC, and ACC. ACC had the largest fraction of multiplexed neurons. (C) Recent value history also affects neuronal firing. The bar plot shows the proportion of neurons encoding the chosen value of the current trial (labeled as N), the previous trial (N − 1), or both. OFC neurons exhibited negative correlation with previous trial value (N − 1, middle), as well as two trials back (N − 2, right), indicating an influence of recent values on current value representation. *Data are from Kennerley et al. (2011).*

THEORY: HOW ARE STIMULUS VALUES COMPUTED?

The previous findings support the hypothesis that vmPFC responses at the time of decision encode a SV signal. But this raises another important and relatively unexplored question: how are these SV signals computed?

One popular theory states that SVs are learned through reinforcement learning and repeated experience with the stimuli, and that the SVs are simply stored in frontal cortex and retrieved at the time of decision (see Chapter 15). Although this process is likely to be at work in settings where subjects repeatedly face a small number of stimuli, it cannot account for the fact that humans easily evaluate novel stimuli.

An alternative view is provided by the *attribute integration model of SV computation*. The model builds on the fact that most stimuli are complex bundles of more basic attributes (e.g., foods can be described by a list of perceptual properties such as size, color, and texture). Using this fact, the model hypothesizes that animals evaluate any stimulus, novel or not, by learning the value of the basic attributes that make up the stimulus and then integrating those attribute values into an overall stimulus value at the time of choice.

This model is illustrated in Figure 8.17. Consider the problem of assigning a value to eating an apple. This consumption act has implications for several basic attributes, or dimensions, such as taste, caloric intake, vitamin and mineral regulation, as well as more abstract dimensions such as health and self-image. Let $d_i(x)$ denote the characteristics of stimulus x for attribute i. The model assumes that:

$$SV(x) = \sum w_i d_i(x), \tag{8.4}$$

for some set of set of attribute weights w_i. In other words, the SV is a linear weighted sum of all considered attributes.

The model has interesting properties. First, it implies that the SVs used to guide choices depend on the attributes that are assigned for each option at the time of choice. This implies that the choice process takes into account the value of an attribute only to the extent that the brain can take it into account in the construction of the decision values. Second, it provides two distinct sources of individual differences: weights

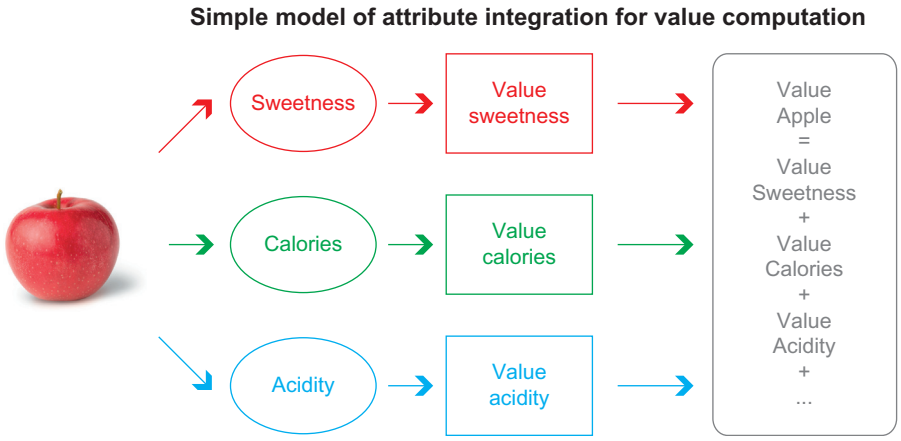

FIGURE 8.17 A simple demonstration of how the brain might integrate various attributes of a potential reward (or punishment). Here, the decision maker considers the sweetness, caloric content, and acidity of an apple. That information is integrated into a value signal for each attribute (middle column, squares). The brain then performs computation (not necessarily linear, as the model has assumed here) to combine each of the attribute values to arrive at a stimulus value for the apple. Presumably, these attributes could be weighted differently across different contexts, such as self-control.

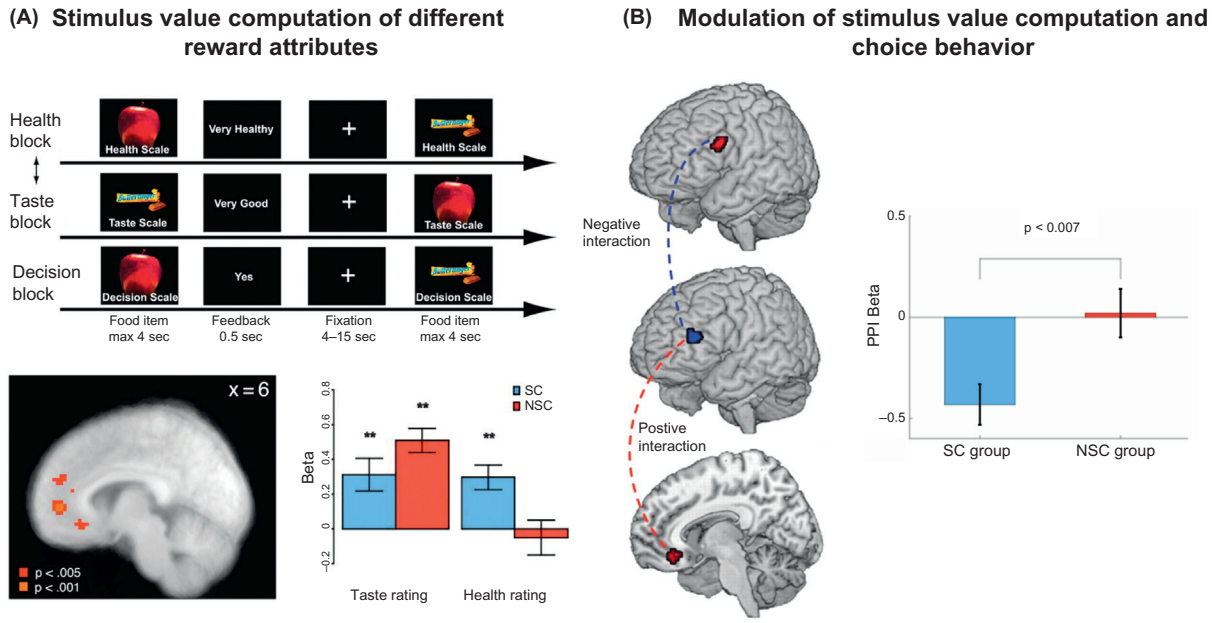

FIGURE 8.18 (A) Top: a self-control task that involves three different blocks: rating food items in terms of healthiness, rating food items in terms of tastiness, and making decisions about willingness to eat the food items at the end of the experiment. Bottom: the willingness to eat the food item was correlated with signal in vmPFC. Taste ratings were strongly correlated with vmPFC activity in both individuals who demonstrated self control (blue) and those who did not (red), while taste ratings were only correlated with vmPFC activity in those who did not exhibit self control. (B) A connectivity analysis a – psychophysiological interaction – identified a path through which the left dlPFC could modulate value computation in the vmPFC. This regulation was present for those displaying self-control (blue), but not for those who's choice behavior did not reflect self-control (red). *Data are from Hare* et al. *(2009).*

might vary because of heterogeneity in preferences for an attribute, or weights might vary because of heterogeneity in a decision-maker's perception of that attribute.

Although much work remains to be done in testing this component of the computational model, several studies have provided supporting evidence for the attribute integration model. One such study looked at dietary choices that involved self-control (Hare *et al.*, 2009). Hungry subjects were asked to make choices about which foods they wanted to have as a snack. Subjects were shown a variety of foods that varied independently in their healthiness and taste. Prior to the choice task, taste and health ratings were collected for each of the foods. As shown in Figure 8.18A, the authors found activity in the vmPFC correlated with both attributes. More importantly, the relative weight that the attributes received in the decision value signals measured in the vmPFC were correlated, across subjects, with the weight given to them in the actual choices made by the same subjects. Interestingly, the study also found that health information was

represented in vmPFC only when a region of left dlPFC was activated. A functional connectivity analysis (Figure 8.18B) suggested that dlPFC might modulate the weight placed on different attributes during value computation in OFC. A follow-up study (Hare *et al.*, 2011a) found that exogenously driven increases in the amount of attention paid to the health attributes (by asking subjects to "consider the healthiness" of the foods) increased the extent to which they were represented in the vmPFC stimulus value signals and the healthiness of the choices.

Additional evidence for attribute integration comes from an fMRI study of charitable decision making (Hare *et al.*, 2010). Subjects were shown descriptions of different charities and had to decide how much to donate to them. The study found that vmPFC responses at the time of decision correlated with behavioral measures of the value that a particular subject assigned to the charities. Moreover, functional connectivity analyses suggest that the vmPFC value signals integrated inputs from anterior insula and posterior superior temporal cortex (pSTC), areas thought to be crucial for social cognition. A related study compared the network involved in making equivalent decisions either for one-self or on behalf of another individual (Janowski *et al.*, 2013). The study found that similar areas of vmPFC encode the SVs in both cases, but that functional connectivity between pSTC and vmPFC is critical when making choices on behalf of another, but not for self.

EVIDENCE FOR A CAUSAL ROLE OF THE STIMULUS VALUE SIGNALS IN vmPFC

Despite the compelling nature of the evidence in favor of the encoding of SV signals in vmPFC, fMRI and neurophysiological measurements are essentially correlational. Just observing that activity in these areas is correlated with SVs is not sufficient to establish that they play a causal role in the choice process. This distinction is important because the theories of choice described in this chapter posit a causal role for the SV signals.

The gold standard for causally linking neural activity to choice behavior would be to precisely manipulate vmPFC responses at the time of choice and test if they lead to changes in the choices that are qualitatively and quantitatively consistent with the model. A recent study, which combined repetitive transcranial magnetic stimulation (rTMS) in dlPFC with fMRI, provides preliminary evidence of this type (Baumgartner *et al.*, 2011). The study measures vmPFC responses at the time of decision by collecting fMRI data immediately after applying rTMS to dlPFC. The results show that rTMS applied to the right dlPFC diminished the activation in both dlPFC and vmPFC, as well as the functional connectivity between them. Most importantly, this neural change was associated with a consistent change in choice behavior.

The only other information currently available regarding the causality of the vmPFC SV signals comes from choice experiments involving clinical populations with focal lesions in regions in and around vmPFC, an area that is sometimes referred to as the ventromedial frontal lobe (vmFC). Several hypotheses discussed in this chapter with respect to vmPFC function are supported by clinical work. In several studies, individuals with vmFC damage consistently violate transitivity in simple choice experiments (Camille *et al.*, 2011a; Fellows and Farah, 2007); individual ability to value-maximize appears to be impaired with vmFC damage. Similar impairments of value comparison have been seen in macaques, with vmFC lesions leading to more erratic choice behavior when available options are closer in value (Noonan *et al.*, 2010). A similar change in behavior has also been demonstrated in intertemporal choice, as damage to vmFC (particularly focal to medial OFC) increased significantly the preference for small-immediate over larger-delayed rewards, effectively steeper discounting of future rewards (Sellitto *et al.*, 2010). Still, while these studies demonstrate consistent impairment of value-based choice across different decision domains, at this point the neurology literature does not definitively conclude whether vmFC – including vmPFC – damage impairs the ability to compute stimulus values, compare stimulus values, or both (Fellows, 2011).

Much evidence points to the ACC working in concert with the vmPFC/OFC to guide value-based behavior, and lesion studies can also contribute to understanding the complex relationship between these regions, a point developed in some detail in Chapter 22. While ACC does frequently appear to encode value signals, it has been shown that these neurons reflect a multiplexed signal that integrates different types of information (Hayden and Platt, 2010; Kennerley *et al.*, 2009). Lesion studies indicate at least two potential relationships. First, lesions in vmPFC/OFC disrupt stimulus–reward but not action–reward association, whereas dACC lesions (which likely include damage to dmPFC) had the opposite effect (Camille *et al.*, 2011b). Second, ACC sulcus lesions in macaques have also been shown to impair the ability to integrate reward history to appropriately guide current behavior (Kennerley *et al.*, 2006). A recent analysis of a large set of humans with focal lesions (Glascher *et al.*, 2012) also established a causal relationship linking vmPFC to value-based decision making, and one linking ACC and dlPFC to functions typically grouped under cognitive control (such as response inhibition and task switching).

Although this body of literature also appears to be converging towards a core set of results, the precise mechanisms at work are not yet known. Clearly, as in most of cognitive neuroscience, much more work has to be done in probing the causality of the various components of the neural mechanism of simple choice. Procedures that probe the root of individual differences will be crucial, as will cutting-edge methods, such as optogenetics (Deisseroth, 2011; Fenno *et al.*, 2011), all with computational modeling to test if the causal effect of these manipulations are consistent with both the qualitative and the quantitative predictions of the theory.

CONCLUSIONS

Understanding simple choices is a foundational goal for neuroeconomics. Simple choices provide the basic framework in which to study the computational and neurobiological basis of decision making. Furthermore, the processes and systems at work in simple choice are likely to contribute to complex choices, such as those involving self-control issues, tradeoffs between self and others, and strategic considerations.

Several pieces of a neural model of simple choice are now in place. A growing body of data supports the hypothesis that vmPFC encodes SVs at the time of choice, that the SV signals use an attention-modulated relative subjective value code, and that these values are integrated using a comparator processes with computational properties that are well-described by the attentional drift-diffusion model (Krajbich and Rangel, 2011; Krajbich *et al.*, 2010). This model provides a firm foundation on which to build our understanding of more complex processes.

Despite the successes in working towards an understanding of simple choice, neuroeconomics remains a young field with many open questions and debates, such as the precise neural mechanisms behind these computations. The good news is further refinements of the model described in this chapter are currently being explored through application of the methods described in this book. Many of the open questions outlined here will be resolved by the time the third edition of this book is written.

One of the central messages of this chapter is the importance of theory and computational modeling. Both of these ingredients are critical for making sense of the body of findings in the domain of simple choice, for helping to design meaningful tests that account for the limitations of our neural measurement techniques, and for correctly interpreting the data. For example, without a full specification of the valuation and choice process, it would be impossible to untangle why neural activity in an area encoding relative stimulus values – which are a precursor and input to the choice process – might also exhibit neural responses that are correlated with the chosen value, which contain post-decision information. The fundamental importance of computational models will only increase as the field moves into more complex forms of choice.

Although the chapter has outlined several points of convergence across studies of simple choice, there remain several pressing questions in the domain of stimulus valuation and simple choice.

What is the Neural Code Used to Represent Stimulus Values in vmPFC?

Thus far, every well-understood system (e.g., vision) is organized around a code that describes how signals are attributed to specific neurons, and how the population activity can be decoded to extract the stored information so that it can be used in downstream computations. For example, retinotopic maps (in which real physical space is represented in the brain using a spatial code) is common in visual sensory and motor systems. Is the computation of SVs organized around a similar code? One natural hypothesis is that vmPFC makes use of an attribute code, so that different units represent the component of value due to the particular combination of attributes that they represent, and that SVs are represented in the population firing rates, and not on the activity of any single unit. If correct, this would help to make sense of the sizable heterogeneity in single unit activity that has been found in single unit studies (Jenison *et al.*, 2011; Kennerley *et al.*, 2011; Padoa-Schioppa and Assad, 2006).

What and How is the Attribute Space Used in SV Computations?

As discussed in the previous section, theory and evidence suggest that SVs are computed by identifying the attributes of stimuli, evaluating them, and then integrating them into a total value representation for the stimulus. The data suggest that the computation of some of these attributes might take place outside of vmPFC, and those values are then passed to vmPFC to be integrated into the final SV signal. However, little is known about what aspect of or how attribute space is employed to carry out these operations.

Computational Roles of PCC, dlPFC, vSTR and Amygdala in Simple Choice

Some studies find that neural responses in some areas are correlated with SVs at the time of choice in a

way that is not easily attributable to arousal, attentional, motor, or prediction error confounds (Litt *et al.*, 2011; Tom *et al.*, 2007). However, in contrast to the vmPFC responses, which are extremely robust, these other areas correlate with SVs in some, but not in all paradigms. This suggests that they play a role in simple choice, but that the computations that they carry out are likely to be different than just encoding SVs. For example, a recent model proposed PCC as a region determining the level of internal or external engagement, as needed for a current environment (Pearson *et al.*, 2011). Resolving this puzzle is one of the most important open questions in the domain of simple choice.

Acknowledgments

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