

Functional Neuroimaging of Intertemporal Choice Models: A Review

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People often forsake a larger reward later for a smaller reward sooner. The process of devaluing the larger, later prize is called temporal discounting or delay discounting, which lies at the core of intertemporal choice. Here, we describe the methodology and findings of research on the mechanisms of intertemporal choice, with a focus on those that utilize functional MRI (fMRI). We consider the neural bases for the most common economic models of intertemporal choice and examine whether these models require neural processes that are common or distinct across types of decision making. Considered as a whole, current research points to potentially distinct contributions from brain systems associated with valuation and with prospective thought, which may be reflected in separable foci in posterior cingulate cortex. Based on open questions in the field, we suggest two core goals for future research: identifying aspects of valuation that are unique to intertemporal choice and evaluating direct or indirect interactions between delay and prize magnitude.

Keywords: delay discounting, intertemporal choice, neuroimaging, fMRI, decision making

Adaptive decision making facilitates the effective consumption and allocation of resources in the pursuit of survival. Some decisions involve choices between two immediately available options that differ in aspects of their value (e.g., relative preferences between attributes) or their probability of occurrence (e.g., risk and uncertainty). However, an important class of decisions involves comparison of options that differ in the time at which they would be available, as when choosing between a smaller reward available immediately and a larger reward only obtainable after some delay. In such intertemporal choice situations, decision makers must adjust the subjective value of the later reward to account for the delay until its arrival.

Because most people judge rewards to be less valuable when obtained later in time, this process is known as temporal discounting. Dysfunctions in intertemporal choice mechanisms are thought to contribute to a wide-range of pathologies of decision making, from failures of planning and investment, and inequities in resource allocation (Angeletos, Laibson, Repetto, Tobacman, & Weinberg, 2001; Laibson, 1997), to pathologies of decision making in addiction (Bickel & Marsch, 2001; Perry & Carroll, 2008), and attention deficit disorder (Critchfield & Kollins, 2001; Plichta et al., 2009).

Individual differences in intertemporal choice can have striking consequences. In a seminal study, Mischel and colleagues examined cognitive and social competencies in children who varied in their ability to delay gratification (Mischel, Shoda, & Peake, 1988). Preschool children were shown a small food reward and then offered the opportunity to obtain a more desirable food reward, if they waited until the experimenter returned to the room to eat the food. Those children who were able to wait longer in this simple paradigm scored better on cognitive, coping, and social competency measures in a follow-up Study 10 years later. Variation in tolerance for reward delay can be attributed to the use of specific cognitive strategies, which points toward im-

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portant directions for improving decision making through a better understanding of intertemporal choice.

There exists a substantial literature on intertemporal choice behavior. As first described by Samuelson (1937) and now replicated and extended in many studies, most individuals willingly sacrifice value to obtain a reward within a shorter time interval (for reviews, see Frederick, Loewenstein, & O'Donoghue, 2002; Kalenscher & Pennartz, 2008; Loewenstein & Prelec, 1992). Such discounting effects are ubiquitous for both primary rewards (e.g., food, juice; Ainslie, 1974; Kobayashi & Schultz, 2008; McClure, Ericson, Laibson, Loewenstein, & Cohen, 2007; Richards, Mitchell, Wit, & Seiden, 1997) and secondary rewards (e.g., money; Thaler, 1981; for review see Loewenstein & Prelec, 1992; Strotz, 1956; Tesch & Sanfey, 2008), although an opposite phenomenon is sometimes observed for aversive stimuli, which can become more negative if farther away in time (i.e., increasingly dreaded; Berns et al., 2006). In Samuelson's formulation, temporal discounting was modeled as an exponential decay function where the subjective value (U), after a delay D , is given by $U = Ae^{-\beta D}$ (Equation 1), where A is the amount of the prize and β is the discount rate. Using an exponential function can be readily shown to be normative, in that it treats all future delay intervals similarly and thus cannot lead to inconsistent or time-varying preferences.

More recent formulations have adopted alternative mathematical frameworks to account for anomalies in intertemporal choice behavior. Most notably, individuals tend to exhibit inconsistent preferences depending on the time until rewards are available (Prelec & Loewenstein, 1991; Thaler, 1981). For example, when choosing between \$100 now and \$110 in 2 weeks, most individuals prefer the smaller and more immediate reward. However, when choosing between \$100 in 36 weeks and \$110 in 38 weeks, nearly all people choose the larger reward—even though this latter scenario will become identical to the former in 36 weeks. This inconsistency, often called the immediacy effect, implies that the mechanism used to calculate intertemporal value shows a strong preference for immediate rewards but a shallower discounting curve at longer times. Proposed al-

ternative models that have these characteristics include a hyperbolic function (Kirby & Marakovic, 1995; Laibson, 1997, 1998; Strotz, 1956) as well as a quasi-hyperbolic function utilizing two exponential decay functions (Loewenstein, 1996; Phelps, 1968; Shefrin & Thaler, 1988).

Given the importance of intertemporal choice – and the ongoing debate about its constituent processes – there has been substantial recent interest in using neuroscience methods to elucidate its underlying mechanisms. Reflecting this interest, more than a dozen recent functional neuroimaging studies (see Table 1) have explored a range of intertemporal choice phenomena. We begin this review with an overview of these studies' methods, with particular focus on how designs used in neuroimaging research differ from those used in behavioral research (both in humans and animals). We then examine the evidence that addresses two core questions about intertemporal choice. How is the value of a delayed reward computed? And, are there aspects of the valuation and decision process that are unique to intertemporal choice?

Together, these questions bear on a topic central to neuroeconomic research: the existence of a common neural currency for reward (Deaner, Khera, & Platt, 2005; Montague & Berns, 2002; Montague & King-Casas, 2007). At one extreme, evidence that intertemporal choice shares valuation and decision mechanisms with other forms of choice (Benzion, Rapoport, & Yagil, 1989; Green & Myerson, 1996) would support the conclusion that subjective value is represented in a single neural currency. Under this perspective, temporal delay is one of many factors that contribute to a representation of value for a choice option, but that the value representation itself has no special qualities because of temporal delay. At another extreme, evidence of fundamental differences between intertemporal choice and other types of choice could lead to the conclusion that intertemporal choice reflects, at least in part, the workings of a separate system for valuation (Chapman & Weber, 2006; Prelec & Loewenstein, 1991). Thus considered, the subjective value of a delayed outcome would only be compared with other value signals at a final step before output (e.g., response selection). As a précis of our conclusions, the current evidence from neuroimaging studies supports an intermediate perspective: that initial aspects of inter-

Table 1
Characteristics of Studies Included in This Review

Reference	Model	Prize	Immediate prize		Delay prize		Delay length	
			Min	Max	Min	Max	Min	Max
McClure 2004	$\beta\delta$	Gift certificate	\$5	\$39	\$6	\$40	0 wk	6 wk
Tanaka 2004	TD	Cumulative direct pay	\$0.09	\$0.26	-\$0.26	\$0.95	0 steps	3 steps
Haniri 2006	k	Hypothetical	\$0.1	\$105	\$100	\$100	0 d	5 yr
Boettiger 2007	ICR	Hypothetical	\$0.7	\$95	\$1	\$100	1 wk	6 mo
Kable 2007	k	Debit cards	\$20	\$20	\$20.25	\$110	6 hr	180 d
McClure 2007	$\beta\delta$	Juice/Water	1 ml	2 ml	2 ml	3 ml	0 min	20 min
Wittmann 2007	$\beta\delta$	Hypothetical	\$0	\$524	\$476	\$524	5 d	10 yr
Ballard 2009	k, $\beta\delta$, & β	Direct pay	\$10	\$10	\$10	\$25	0 d	180 d
Bjork 2008 (VBM)	k	Direct pay	\$0.25	\$10	\$10	\$10	0 d	1 yr
Ersner-Hersfield 2008	k	Direct pay	\$0.01	\$10.5	\$10	\$10	0 d	1 yr
Hoffman 2008	k	N/A	\$1	\$99	\$100	\$100	0 d	1 yr
Luhmann 2008	β	Cumulative direct pay	\$0.1	\$0.2	\$0.1	\$0.2	1 s	9 s
Shamosh 2008	AUC	Hypothetical	\$10	\$40,000	\$200	\$40,000	1 mo	8 yr
Weber 2008	k	Gift certificate	\$5	\$7	\$6	\$12.6	0 mo	5 mo
Clithero 2009	k	Gift certificate	NA	NA	\$15	\$50	1 wk	16 wk
Plichta 2009	ICR	Direct pay	\$6.86	\$54.84	\$7.2	\$82.27	0 wk	4 wk
Gregorios-Pippas 2009	k & β	Cumulative direct pay*	\$0	\$20*	\$20	\$20	4.0 s	13.5 s

Note. Prizes paid in foreign currencies were converted to US dollars using the average exchange rate from the year before the publication of the study. TD = temporal difference; ICR = impulsive choice ratio; AUC = area under the curve; Hypo. = hypothetical; N/A = not applicable.

* Paid only a fraction of the total cumulative.

temporal valuation reflect neural mechanisms that differ from that of other forms of choice, but that the associated value signals are later represented within a common reward system.

Methodological Differences in Delay Discounting Studies

The effects of temporal delay upon subjective value are, considered generally, predictable and intuitive: as the delay until a reward increases, its subjective value decreases. The generality of this phenomenon – which operates across a wide range of rewards and time scales – has allowed researchers to use a broad range of methods, reward modalities, choice options, and analysis parameters in their experiments. Here, we describe the approaches used in published studies that have used functional neuroimaging methods (in all cases, functional MRI, or fMRI) to investigate the neural basis for delay discounting. Even within this restricted sample, there has been a great deal of diversity in the methods used to isolate the effects of delay on rewards, despite the shared interest in a nominally similar cognitive process. Listed in Table 1 are all (to our knowledge) published neuroimaging studies of intertemporal choice, along with their key methodological parameters.

Discounting Functions

As noted above, while the effects of delay upon value can be modeled normatively using a single exponential decay function, more complex functions are needed to describe actual choice behavior (Fudenberg & Levine, 2006; Kalenscher & Pennartz, 2008; Loewenstein, O'Donoghue, & Rabin, 2003; O'Donoghue & Rabin, 2000; Ok & Masatlioglu, 2007). So far, neuroimaging studies of intertemporal choice have modeled the effects of delay using five different approaches: a single exponential decay function (3 studies), a dual exponential decay function (i.e., the beta-delta model; 4 studies), a temporal difference model (i.e., performing a multiple regression analysis using a temporal difference model with a decay parameter ranging from 0 to 0.99; 1 study), a hyperbolic function (i.e., calculating a k value; 8 studies), and some measure of the proportion of choices of

the more-delayed option (3 studies). The parameters for these functions are normally calculated on an individual-by-individual basis by offering each participant a series of choices and then determining pairs of immediate and delayed rewards with equivalent value. Alternatively, some studies have estimated the parameters that best fit the collection of choices made by the participant. In determining discounting functions, the majority of the studies (nine) vary the magnitude of both the delay and immediate prize, while the remainders vary the magnitude of only one or neither of the two prizes. The practice of varying only the delay prize (fixed immediate reward) elicits greater discounting from participants than only varying the immediate prize (fixed delay reward; Tesch & Sanfey, 2008).

Prize Modalities

There has been remarkable variability in the reward parameters used within neuroimaging studies of intertemporal choice. Some of this diversity is driven by differences in delay parameters. To elicit variability in intertemporal choice, it is necessary to structure delays and prize magnitudes so that participants sometimes choose the delayed option and sometimes choose the immediate option. Thus, longer delays are often correlated with larger prizes. However, prize choice is also driven by the payment method. For reference, nearly all such studies within behavioral economics have examined choices for monetary rewards, the majority of which have involved hypothetical rewards (see Frederick et al., 2002, for review). Within our study sample, the prizes offered included direct monetary payments (cumulative or random, 7 studies), gift certificates or debit cards (4 studies), hypothetical monetary payments (4 studies), or juice/water (1 study). The range of symbolic prize magnitude, for a single trial, across studies is very large, from a minimum of \$0.01 (in Ersner-Hershfield, Wimmer, & Knutson, 2008) to a maximum of \$40,000 (in Shamosh et al., 2008). Studies using a hypothetical payment method have a median maximum prize of \$312 while those paying directly (cash or gift certificate, usually on a few randomly chosen trials) have a median maximum prize of \$32.50. Those studies using a cumulative direct pay method have the smallest (per trial) median maximum prize (\$0.95).

We note that there are examples of prior behavioral research that provide indications that hypothetical prizes can be treated differently than real prizes, especially at short delays (Camerer & Hogarth, 1999; Smith & Walker, 1993), though there are also examples where no difference was found (Baker, Johnson, & Bickel, 2003; Johnson & Bickel, 2002; Lagorio & Madden, 2005; Madden, Begotka, Raiff, & Kastern, 2003; Madden et al., 2004). Random single-trial payments have also been shown to evoke different discount rates than cumulative payment methods (Kagel & Roth, 1997). Most neuroeconomic studies of risky choice, for comparison, now use a standard payment scheme: choices involve real monetary rewards in the range of a few tens of dollars (or equivalent in other currency) and pay participants for a subset of their choices, selected randomly; see (Clithero, Carter, & Huettel, 2009; Hsu, Bhatt, Adolphs, Tranel, & Camerer, 2005; Huettel, Stowe, Gordon, Warner, & Platt, 2006) for examples. No such convergence exists for research on intertemporal choice. We return to the motivation behind this diversity in the summary paragraph below.

Delay Intervals

Similarly, there has been little consistency in temporal interval across studies. The majority of neuroimaging studies included in this review (12 studies) use delays in the range of weeks to years, with the remainder using much shorter delays of seconds to minutes for rewards obtained during the experiment itself (McClure et al., 2007) and for symbolic rewards that are accumulated (Gregorios-Pippas, Tobler, & Schultz, 2009; Luhmann, Chun, Yi, Lee, & Wang, 2008; Tanaka et al., 2004). While the former range is generally compatible with that used in behavioral economics research, it differs dramatically from that of the large animal literature on delay discounting, which normally uses delays on the order of several seconds (Hayden & Platt, 2007; Kalenscher et al., 2005; Kalenscher et al., 2004; Rosati, Stevens, & Hauser, 2006; Stevens, Hallinan, & Hauser, 2005; Stevens, Rosati, Ross, & Hauser, 2005). These very different time scales may involve different neural substrates (Lane, Cherek, Pietras, & Tcheremissine, 2003). As an example, a study by Wittmann and colleagues (2007) contrasted delays (for hypothetical rewards) of less than one

year with delays of greater than one year, finding that regions involved with reward evaluation, among others, differentiated these two categories. Moreover, using real but nonimmediate rewards (i.e., those delivered after the participant leaves the laboratory session) risks incurring transaction costs that can influence subjective value and that are not present in animal research. Note that, in contrast, McClure and colleagues have used both monetary rewards with delays of weeks (McClure, Laibson, Loewenstein, & Cohen, 2004), and juice rewards with delays of minutes (McClure et al., 2007), and report relatively similar patterns of activation across the two studies.

The variability in models, payment methods, and delay intervals used in intertemporal choice studies has surely contributed to differences in their results. Yet, it is important to note that the use of a standardized set of conditions poses significant limitations. For example, when studying impulsivity in choice, the promise of an abstract prize later may not elicit the desired behavior. Utilizing substantive prizes that are large enough to elicit a tradeoff at longer delays may also raise ethical concerns. Nevertheless, consistency in methods may often improve connections to other research without compromising the purpose of the study.

Summary of Neuroimaging Studies:

ALE Analysis

In spite of the array of methods catalogued above, studies of delay discounting show substantial overlap. In order to provide a coarse representation of the regions of the brain consistently involved in studies of delay discounting, we performed activation likelihood estimation (ALE) using GingerALE (Laird et al., 2005). We included activation peaks from each of the studies listed in bold in Table 1. Three studies were excluded because they used ROI-based analyses (Bjork, Momenan, & Hommer, in press; Clithero et al., 2009; Gregorios-Pippas et al., 2009). One study was excluded because its coordinates were reported in an unconventional space (Hoffman et al., 2008). Analysis of 378 foci in the remaining 13 studies using 10,000 permutations (10 mm FWHM) returned 25 significant clusters (see Table 2), representing regions that were more likely to be activated during tasks that involve delay dis-

Table 2
Results of ALE Analysis

Cluster	Volume, mm ³	Cluster peak (TAL)			Network
		x	y	z	
Medial prefrontal cortex	9,888	-2	40	18	Both
Ventral striatum	9,256	14	10	0	VAL
Posterior cingulate cortex	1,976	-8	-36	36	VAL
Right insula (R)	1,824	36	18	-2	VAL
Temporal parietal cortex (L)	1,776	-48	-66	14	CN
Splenial posterior cingulate	1,736	-2	-50	20	CN
Left insula (L)	1,328	-30	18	-6	VAL
Left inferior PFC (L)	1,016	-50	0	12	Neither
Left inferior PFC (L)	1,000	-42	4	30	Neither
Left temporal pole (L)	800	-46	4	-24	Neither
Posterior parietal cortex (L)	688	-28	-60	44	Neither
Posterior parietal cortex	656	26	-60	46	Neither
Occipital cortex	576	-12	-88	10	Neither
Inferior parietal lobule	520	-50	-52	24	CN
Occipital cortex	384	12	-82	14	Neither
Left superior frontal gyrus	368	-18	24	42	Neither
Somatosensory cortex	344	30	-42	50	Neither
Lateral orbitofrontal cortex	336	40	46	-12	VAL
Inferior parietal lobule	248	56	-42	26	Neither
Right anterior inferior PFC	232	48	34	10	CN
Right anterior inferior PFC	216	46	48	6	CN
Middle temporal gyrus	208	-64	-46	4	CN
Left posterior insula	184	-30	0	6	Neither
Somatosensory cortex	168	-44	-32	46	Neither
Midbrain	160	6	-22	-8	VAL

Note. Significant clusters from an anatomical likelihood analysis of 13 delay discounting fMRI studies. VAL indicates this region is normally part of the value network. CN indicates this region is normally part of the core network. PFC = prefrontal cortex; L = left; R = right.

counting (see Figure 1). Consistent with delay discounting functioning as a complex decision, Table 2 shows areas associated with a wide range of processes. Figure 1 shows regions included in a network of areas known to be sensitive to value (ventral striatum, medial prefrontal cortex, orbitofrontal cortex, anterior insula; Gottfried, O'Doherty, & Dolan, 2003; Knutson, Adams, Fong, & Hommer, 2001; Montague & Berns, 2002; O'Doherty, Deichmann, Critchley, & Dolan, 2002) or subjective value (PCC; Kable & Glimcher, 2007), shown colored in red. Regions shaded in blue are often associated with a "core network" (Spreng, Mar, & Kim, 2009) that supports prospective processes like autobiographical memory, theory of mind, and planning for the future. These included inferior prefrontal cortex, medial prefrontal cortex, temporal-parietal cortex, and peri-splenial posterior cingulate. Although the list of contrasts included in the ALE analysis were as diverse as

the methodologies discussed above, these two networks could be reliably extracted.

In summary, the most obvious feature of the neuroimaging literature on intertemporal choice is its methodological variability. Nevertheless, two sorts of research questions have recurred throughout this sample. First, there has been consistent interest in the neural mechanisms underlying the construction of value for temporally delayed prizes, both in how it relates to specific functional forms and whether distinct brain systems are engaged by temporal delay. Second, intertemporal choice has been set forth as a prototypic example of how cognitive control can override impulsive, reward-seeking choice (cf., Kahneman & Tversky, 1979), with concomitant interest in the contributions of neural control systems for selection of delayed outcomes. We discuss how neuroimaging data can bear on these questions in the following sections. Finally,

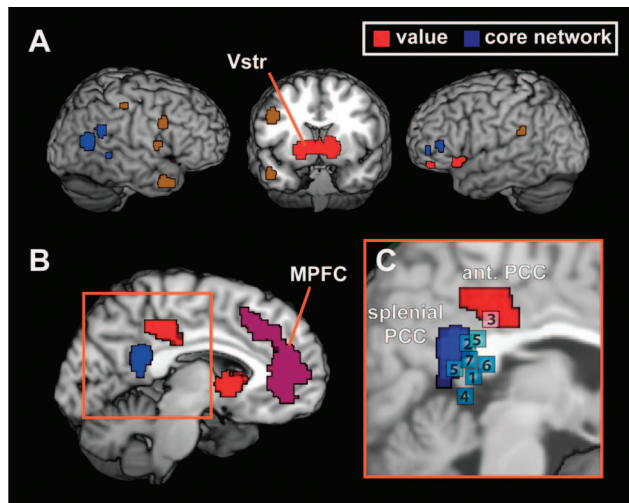


Figure 1. ALE Analysis of Delay Discounting fMRI Studies. Shown in (A) are clusters identified as associated with intertemporal choice, based on an activation likelihood estimate (ALE) meta-analysis of 13 delay discounting studies (see text for details). Regions often associated with a value network are shaded in red, while regions associated with a core network for self-directed thought are shaded in blue. Within the posterior cingulate cortex (B), there is evidence for a division between a more anterior and dorsal region of posterior cingulate cortex (PCC) that is associated with value and a retrosplenial region associated with self-directed and prospective thought (C). Shown in boxes are centroids of PCC activation from seven relevant studies: 1 Ballard & Knutson, 2009; 2 Harrington et al., 2004; 3 Kable & Glimcher, 2007; 4 Luhmann et al., 2008; 5 Spreng et al., 2009; 6 Weber, & Huettel, 2008; 7 Wittmann et al., 2007. Vstr—ventral striatum, MPFC – medial prefrontal cortex, PCC – posterior cingulate cortex.

we consider the implications of the current literature for methodology and theoretical grounding of future studies. Considered broadly, nearly all existing studies use paradigms drawn from the behavioral economics literature, such that decisions are regarding mid-sized to large monetary rewards obtainable over a period of weeks to years. Yet, within this broad category there exist numerous differences that make comparison across studies challenging: few studies have adopted such similar procedures that methodological differences can be ruled out as explanations of their different results. We will return to the implications of this methodological variability for future research at the end of this review.

How Is Value Constructed for Temporally Delayed Prizes?

Anomalies in human intertemporal choice behavior suggest potential constraints for the

underlying neural mechanisms. Samuelson's initial model described delay discounting using an exponential decay function (see Equation 1), an elegant and simple solution that utilized the math common in interest calculation at the time. Yet, numerous violations of this model are evident (Prelec & Loewenstein, 1991; Thaler, 1981), some noted by Samuelson at the time of the original work. Collectively, these violations imply a function with a much steeper discounting over short time scales. Functional neuroimaging studies have sought brain regions whose activation tracks specific parameters of these functions and, therefore, potentially contribute to valuation. Because different studies have adopted rather different functions for explaining their observed behavior, there have been areas of disagreement within the literature that point to clear avenues for future experimentation. Here, we present two proposed models of intertemporal choice, quasi-hyperbolic and hyperbolic discounting, using studies from McClure and colleagues (2004) and Kable and Glimcher (2007).

These studies differ in many aspects of their methods; for example, they differ in the amount of training participants receive. Even so, they provide a unique opportunity to contrast the neural substrates postulated to support distinct models of intertemporal choice.

Quasi-Hyperbolic Discounting

In an early fMRI study of intertemporal choice, published in 2004 by McClure and colleagues (McClure et al., 2004), participants chose between pairs of real monetary rewards that differed in their value (over a range of a few tens of dollars) and delay before delivery (over a range of a few weeks). To guide their analyses, the authors adopted a two-process framework that models discounting using a quasi-hyperbolic function for subjective value (U), for a prize of amount A , at a given delay D , as $U = A\beta\delta^D$ (Equation 2; see Laibson, 1997; Loewenstein, 1996; Shefrin & Thaler, 1988). Note that this perspective matches well to the pervasive dual-systems account of behavioral control (Bechara, 2005; Ernst & Paulus, 2005; Kahneman, 2003; Loewenstein, 1996). Their analyses sought brain regions whose activation was consistent with each of two model parameters. The first parameter, β , is also referred to as the “hot” or visceral system. It reflects a strong preference for immediate rewards when compared to any delay. Through a contrast between decisions involving an immediately available reward and those involving only delayed rewards, they found that regions normally associated with value representation, such as the ventral striatum, medial prefrontal cortex, medial orbitofrontal cortex, and posterior cingulate, increased with the presence of an immediate reward. The second parameter, δ , is also referred to as the “cold” or rational system. It produces a shallow discounting rate (and thus reduced discriminability between reward values) at longer delays; within their analyses, delta-related regions were defined based on having similar activation levels regardless of intertemporal delay. This approach revealed activation within dorsolateral prefrontal cortex, parietal cortex, lateral orbitofrontal cortex, as well as regions associated with motor and visual processing.

The results of McClure and colleagues have been highly influential, in that they have been

interpreted to provide evidence for two conclusions: generally, that the value of a delayed option depends on the interaction between two distinct sets of neural systems and, specifically, that impulsive choices reflect an overactivation of the reward system (compared to control mechanisms). Moreover, the basic results were replicated by the same group in a 2007 paper (McClure et al., 2007) that used liquid rewards (juice and water). In this latter study, participants were offered a choice between a small amount of a liquid reward now, and an amount as much as three times larger after a maximum delay of 20 minutes. Utilizing a beta/delta model, they find reward circuitry activation for choices involving an immediate reward and lateral prefrontal and parietal activation for trials comparing delay prizes. They also find no difference between striatal BOLD responses to prizes delayed 10 minutes and those delayed an amount comparable to the first experiment. These results have been interpreted as strong neural evidence in favor of a two-component model of intertemporal choice.

Hyperbolic Discounting

An alternative perspective was advanced by Kable and Glimcher (2007) who used experimental procedures largely similar to those of McClure and colleagues (McClure et al., 2004) but began with a different framework: they hypothesized that neural systems for valuation reflected a single hyperbolic discounting function that operated regardless of delay interval

$$U = \frac{A}{1 + kD} \text{ (Equation 3, } U = \text{ subjective value,}$$

A = prize amount, D = delay magnitude, k = discounting parameter; Laibson, 1997; Mazur, 1987; Strotz, 1956). For each participant, they measured discounting preferences based on independent behavioral sessions (and subsequently matched to data from the fMRI session). Their key analyses compared distinct functional forms to determine which best matched activation in brain regions associated with valuation. They found that subjective value, as estimated for each participant using a single-parameter hyperbolic decay function, was very well matched to activation in ventral striatum, ventromedial prefrontal cortex, and posterior cingulate cortex. They also demonstrated that the hyperbolic function fit their

fMRI data better than both a single-component decay function as well as a more shallow decay function similar to the delta component of the beta-delta model. Control analyses excluded potential confounding factors ranging from absolute amount of reward to delay until reward delivery.

Favoring the simplest interpretation of these results, Kable and Glimcher concluded that the value of a delayed outcome was represented in canonical reward-related brain regions, whose activation was largely consistent with a standard hyperbolic discounting model. (See Glimcher, Kable, & Louie, 2007, for additional discussion by the same authors about the potential importance of these results for economic modeling.) Hyperbolic discounting functions have been shown to have a number of advantages over other models of discounting (Kirby & Marakovic, 1995). The conclusion that computation of the value of a delayed outcome relies on similar mechanisms as other rewards is consistent with work by Hariri and colleagues (Hariri et al., 2006), which shows that reward sensitivity in the ventral striatum scales with a participant's hyperbolic discounting coefficient.

The results of Kable and Glimcher provide compelling evidence that delay valuation relies on the same neural mechanisms as do other types of valuation. Nevertheless, two main caveats are in order. First, analyses of this type need extensive and well-distributed data to make fine distinctions between functional forms (Berns, Laibson, & Loewenstein, 2007). Acquisition of such data requires a sampling process that grows very rapidly with small increases in coverage and resolution of the prize parameter space. Even comprehensive analyses like that of Kable and Glimcher (Kable & Glimcher, 2007) only imperfectly sample the full parameter space: they have relatively few participants and, thus, limited examples of discounting parameters, and they present only a limited set of stimuli to define distribution biases. For example, changes in the initial delay to prize have not been described in the literature (but see Glimcher et al., 2007). Moreover, different functions do not lead to drastically different predictions for the majority of intertemporal choice scenarios, reflecting the general similarity between the hyperbolic and quasi-hyperbolic functions. Because of this imprecision, results from other studies, such as increased striatal activation to

relatively short delays (Wittmann et al., 2007), would be consistent with either model. A potential strategy would be to focus model fit tests to only the specific range of values where strong discrepancies are predicted.

Second, the observed activation in value-relevant brain areas describes a point in the construction of an intertemporal choice, not the entire mechanism. Other processes, such as an impulsive choice system, could have upstream or downstream influences on a subjective-value representation. As summarized by Tesch and Sanfey (2008), a range of behavioral effects can modulate subjective value in intertemporal choice: a prize magnitude effect, greater discounting for smaller rewards (Raineri & Rachlin, 1993; Thaler, 1981); an effect of the number of choices, more choices increases discounting (Read, 2001); an order effect, increasing sequences are valued more than decreasing sequences (Loewenstein & Sicherman, 1991); a preference for speeding up rather than slowing payment schedules (Loewenstein, 1988); a preference for distributed rewards (Loewenstein & Prelec, 1993); an effect of reward type, food is discounted more strongly than money (Odum & Rainaud, 2003); and an effect of reward valence, gains are more steeply discounted than losses (Thaler, 1981). In addition, discounting preferences can be modified by distraction (Mischel, 1972). There are also cases where the mental state of the participant preceding the choice modulates discounting (summarized in Berns et al., 2007; Montague & King-Casas, 2007). Discounting rates are increased by deprivation of self control (Baumeister & Heather-ton, 1996), when emotionally or sexually aroused (described in Loewenstein, 1996), or when smokers are deprived of nicotine (Field, Santarcangelo, Sumnall, Goudie, & Cole, 2006; Mitchell, 2004). Schweighofer and colleagues (2006) propose a more general conclusion that the participant's choices reflect the optimal discounting function for the task. Collectively, these phenomena make it difficult to argue for a single hyperbolic discounting function utilized in the brain. Very recent data also pose difficulties for the simple conclusion that hyperbolic discounting behavior reflects hyperbolic activation of the reward system. Gregorios-Pippas, Tobler, and Schultz (2009) found that an exponential decay function was a slightly better

model of activity in the ventral striatum during delay discounting than a hyperbolic function.

Are There Neural Mechanisms Specific to Intertemporal Choice?

In biological systems, selection pressures can lead to coopting of existing mechanisms for new purposes. The use of a single mechanism for valuation would provide significant advantages (Montague & Berns, 2002; Sugrue, Corrado, & Newsome, 2004), most notably by providing a common currency for comparisons between different forms of reward (Klein, Deaner, & Platt, 2008). As described above, there exists substantial evidence that brain regions associated with the evaluation of immediately obtained primary and secondary rewards (Delgado, Nystrom, Fissell, Noll, & Fiez, 2000; Knutson et al., 2001; Schultz, Dayan, & Montague, 1997), both sure and probabilistic (Kuhnen & Knutson, 2005), are modulated by aspects of rewards obtainable after some delay, including both the relative immediacy of those rewards (McClure et al., 2007; McClure et al., 2004; Wittmann et al., 2007) and the subjective value of those rewards (Kable & Glimcher, 2007). One natural conclusion from these findings is that intertemporal choice merely reflects one application of a general-purpose decision-making mechanism. In this section, we evaluate an alternative (and more nuanced) perspective: that distinct brain regions play important roles in intertemporal choice, compared to other forms of decision making.

Explaining intertemporal choice using only mechanisms for reward evaluation would pose several challenges. First, a strict common-currency explanation does not readily account for modality-specific manipulations of value, despite examples of delay-specific framing effects as introduced above (Berns et al., 2007; Tesch & Sanfey, 2008). Second, that a common currency exists at relatively late stages of processing – which seems tautological given individuals' ability to compare distinct rewards – does not preclude initially separate computations of value that are then combined at a later stage for comparison purposes. Rewards that are delayed in time are likely to be represented and evaluated, at least initially, through different mechanisms. Prize types differ in enough aspects of their representation that not all neural substrates

leading to the common currency map can be consistent across them. Given these and similar concerns and the results described in the previous section, the cardinal outstanding question for neuroimaging studies of intertemporal choice is not “How is subjective value represented?” but “Are there aspects of subjective value computation and comparison that are specific to intertemporal choice?”

We note that prior behavioral studies provide equivocal answers to this latter question. Some theorists have noted that all forms of reward discounting, whether intertemporal or probabilistic, may share aspects of calculation and comparison (Cardinal, 2006; Green & Myerson, 2004; Prelec & Loewenstein, 1991). As examples, rewards become less valuable when associated with risk or ambiguity, as can be modeled using simple decay functions (Von Neumann & Morgenstern, 1944). One perspective is that delay discounting involves estimation of risk: each time point leading up to delivery of a prize can be modeled with a constant hazard; therefore, more temporally distant prizes are less likely to be obtained. Probabilistic prizes, conversely, could be modeled according to their estimated delay until delivery: lower probability prizes require more attempts and, therefore, a longer delay before they are obtained. Moreover, some anomalies are common across probability and delay discounting models (Prelec & Loewenstein, 1991); probabilistically certain outcomes are overvalued (Allais, 1953), just like immediately available outcomes. There are notable exceptions, however. Increasing magnitude of reward usually has opposite effects on probability and delay: large rewards reduce the immediacy effect but increase the certainty effect (Chapman & Weber, 2006; Prelec & Loewenstein, 1991; Rachlin, Brown, & Cross, 2000; Weber & Chapman, 2005). In addition, relationships between an individual's risk preferences and delay preferences have been found in some cases (Crean, de Wit, & Richards, 2000; Myerson, Green, Hanson, Holt, & Estle, 2003; Reynolds, Karraker, Horn, & Richards, 2003) but not in others (Ohmura, Takahashi, & Kitamura, 2005; Reynolds, Richards, Horn, & Karraker, 2004).

Three recent fMRI studies have combined intertemporal and risky choice within the same paradigm. Weber and Huettel examined differences in the neural substrates of risk and delay

valuation (Weber & Huettel, 2008) by asking participants to choose between pairs of monetary outcomes differing in their delay or their risk. (Note that all choices were within-modality; participants never compared a delayed but certain outcome to a probabilistic but immediate outcome.) Their results indicated that there was some differentiation in the regions of the brain supporting each type of valuation. Decision making involving risk produced greater activation, compared to delay and control tasks, in a number of regions, including the posterior parietal cortex, the dorsolateral prefrontal cortex, the anterior insula, the anterior cingulate cortex, and the orbital frontal cortex. These regions largely overlapped with those reported in previous studies of risky choice (Dickhaut et al., 2003; Hsu et al., 2005; Huettel et al., 2006; Kuhnen & Knutson, 2005; Paulus, Rogalsky, Simmons, Feinstein, & Stein, 2003; Rogers et al., 1999). Decision making involving delay evoked greater activation, compared to risk and control tasks, in the posterior cingulate cortex. A similar regional differentiation was observed in a second study from the same laboratory that focused specifically on valuation of delayed or probabilistic rewards. Using a pattern-classification analysis derived from machine learning, Clithero, Carter, and Huettel (2009) found that patterns of activation within voxels in posterior parietal cortex (and, secondarily, within posterior cingulate cortex) uniquely predicted whether a participant was valuing a delay or risk prize, even when controlling for the overall activation level within a brain region.

In a third study examining potential differences between risk and delay discounting, Luhman and colleagues (2008) asked participants to choose between a small prize available immediately, with certainty, and a larger prize available either with some risk or with both risk and a temporal delay. The probability that a prize would be received was represented using a set of one to nine squares, each of which had a constant hazard of 0.1. In the delay condition, the same squares indicated both the risk previously described and a delay of 1 second per square. Luhman and colleagues found that activity in posterior cingulate correlated with the addition of the delay condition, an aspect of the risk and delay valuation process that was not common to both. This finding agrees with the

results of Weber and Huettel (2008). Also consistent with a role for the posterior cingulate in delay prize valuation, Wittmann and colleagues (2007) note a correlation between posterior cingulate activity and a participant's choice of the delayed option. These studies provide strong evidence that activity in the posterior cingulate is related to delayed, but not risky, prize valuation.

If activity in the posterior cingulate is specifically relevant to the valuation of temporally delayed prizes, what components of delay prize valuation could be carried out there? One possibility is that activity in the posterior cingulate correlates with the subjective value of a delayed reward but not the subjective value of a risk reward. In fact, Kable and Glimcher found evidence of posterior cingulate activity that correlates with subjective prize value (Kable & Glimcher, 2007). A second and even more intriguing possibility is that the posterior cingulate lies earlier in the delay prize valuation pathway, computing the primitives of delayed prize valuation. If this is true, we would then expect activity in the posterior cingulate to correlate with the temporal component of the delay prize or the objective delay prize magnitude, but not subjective value. Though Kable and Glimcher demonstrated correlations with subjective value in the posterior cingulate, activation in an adjacent and possibly distinct region may correlate with its more primitive components (see Figure 1B and C).

Evidence of objective prize magnitude and temporal delay sensitivity was presented in a very recent paper by Ballard and colleagues (Ballard & Knutson, 2009). Dissociating temporal delay and objective prize magnitude, they show that the peri-splenial aspect of the PCC responds to the displayed value of the prize (the objective value; Ballard & Knutson, 2009). They also found evidence of temporal sensitivity in the peri-splenial aspect of the posterior cingulate. Specifically, increases in this region's responses to temporal delay were negatively correlated with the participants' individual discount parameters. More evidence of temporal sensitivity in the peri-splenial posterior cingulate was presented in a study by Ersner-Hershfield and colleagues (2008). Their participants viewed a series of adjectives, evaluating how relevant some were to their current self and how relevant others were to a future (envi-

sioned) self. The authors found that a similar region in the posterior cingulate is more active when considering a person in the present than when considering a person in the future. A similar portion of the posterior cingulate is also implicated in the encoding of time intervals (Harrington et al., 2004), see Figure 1C. Given these commonalities, future work will need to better incorporate cognitive neuroscience research into time representation (Buhusi & Meck, 2005).

Adjacent representation of subjective value and delay prize valuation primitives provides a convenient location for the construction of delayed prize value primitives and their interaction with a broader system for common currency. This intriguing possibility provides a target for future studies seeking to identify the mechanism of interaction between delay prize representation and subjective value.

Unanswered Questions and Future Directions

Building on the structure provided by a rich behavioral literature, neuroimaging data could, in principle, not only provide concrete descriptions of abstract model features but also even provide a means for adjudicating between similar models. Indeed, the series of innovative studies described in this review have collectively made significant progress toward this goal. Regions of the brain that show significant correlations with aspects of intertemporal choice, such as the striatum, posterior cingulate cortex, insula, and medial prefrontal cortex, provide a solid basis for further elaboration. Even so, the core questions identified at the outset of our review – and targeted by the studies we describe – remain only imperfectly answered. We conclude by identifying three outstanding challenges for future research on intertemporal choice, along with some suggestions for methodological improvements to meet those challenges.

Distinguishing Models and Their Constituent Processes

What steps should researchers take to better test the distinguishing features of competing models? While there is now general acceptance

that a normative exponential model cannot account for real-world discounting behavior (see Ballard & Knutson, 2009; Gregorios-Pippas et al., 2009; Schweighofer et al., 2006, for possible exceptions), there exists no consensus about its replacement. Hyperbolic models of discounting are both simple and well-fit to fMRI data in at least some experiments (Glimcher et al., 2007; Kable & Glimcher, 2007). However, hyperbolic models leave significant portions of behavior unexplained (such as the framing and context effects described above). And, other researchers have found little or no difference between how well distinct functions fit fMRI data (Ballard & Knutson, 2009; Gregorios-Pippas et al., 2009) or have found that the best model depends on the experimental conditions (Schweighofer et al., 2006). Dual-system models match intuitive descriptions of intertemporal choice: Everyone would prefer to have the larger prize sooner but most exercise the necessary restraint to make what they believe to be a smarter choice, often choosing the delayed prize. This self restraint has limits; it is not an unlimited resource, and there are many examples (see the previous sections) where discounting can be altered by depleting self restraint before a choice. These counterpoints do not make the models mutually exclusive. It is difficult to imagine a neural mechanism that would predict framing effects specific to delay discounting that does not also provide a delay-specific representation of value. A likely possibility would be that there are secondary influences on early and unique aspects of the delayed prize value calculation. This value could then be passed on to a common currency system where different value types are compared. Given that anomalies of delayed prize valuation remain unexplained, more complex models seem necessary. A number of promising candidates await testing (e.g., Fudenberg & Levine, 2006; Kalenscher & Pennartz, 2008; Loewenstein et al., 2003; O'Donoghue & Rabin, 2000; Ok & Masatlioglu, 2007).

The diverse set of methods used in fMRI studies of intertemporal choice has not only provided a wealth of potential conclusions but also strengthened (through converging data) those findings that have been consistent across studies. Yet, specific replications of those findings are necessary. An approach that makes great strides toward reconciling studies whose

results differ is a direct comparison of the fit of the alternate economic models to neural data, see Kable and Glimcher (2007) as well as Gregorios-Pippas, Tobler and Schultz (2009) and Ballard and Knutson (2009) for examples. In order to facilitate comparisons across studies, we recommend that, for most research questions, future experiments should use the most common parameters and design methods: delay periods in the range of weeks; real payments, through a subset of the trials completed; variance of both the immediate and future prize amount; and variance in the order and placement of prizes presented. We do, however, again note that there are constraints that may require deviations from these guidelines (e.g., for juice rewards, a delay of weeks would be unreasonable).

Finally, we note that functional neuroimaging data are not, in themselves, sufficient for distinguishing models of intertemporal choice. At root, the empirical data needed to establish whether discounting functions follow a hyperbolic, quasi-hyperbolic, or some other function will come from rigorous behavioral testing. What functional neuroimaging data can provide, however, is the ability to evaluate what classes of models are biologically plausible and, thus, are good candidates for future behavioral testing (see Clithero, Tankersley, & Huettel, 2008, for additional discussion). As an example, Delgado and colleagues have demonstrated that a neurobiologically based model can motivate the design of auctions in a study of overbidding behavior (Delgado, Schotter, Ozbay, & Phelps, 2008). Neuroimaging (or other neuroscience) data could also provide needed constraints for any model: identifying conditions under which their parameters might change, predicting the effects of additional manipulations (e.g., time pressure, depression), and providing insight into individual differences (e.g., effects of aging).

Improving the Connection to Animal Research

Many of the most successful areas of neuroscience (e.g., vision science, memory) have involved close interaction between human and animal research. While no studies have heretofore demonstrated intertemporal choice in animals at delays similar to typical human experiments (i.e., days or longer), research suggests

that some animals possess cognitive capacities that are potentially homologous to the mechanisms of delay discounting. As examples, apes show long-term planning by retaining tools for use 14 hours later (Mulcahy & Call, 2006) but have not yet demonstrated that they can reject an immediate prize for a larger one that will occur more than a few minutes later (Chimps 123s; Rosati, Stevens, Hare, & Hauser, 2007). Corvids and many other animals cache food for much later use (Raby, Alexis, Dickinson, & Clayton, 2007), albeit in a largely stereotyped format. In addition, intertemporal choice is strongly affected by the loss of portions of the prefrontal cortex (Bechara, Tranel, & Damasio, 2000), which may have very different functional properties and connectivity in human and nonhuman animals. Directly relevant to this point, the relative volume of human prefrontal cortex is correlated with smaller discounting rates (Bjork et al., 2009). There is a disconnect between this result and those described in the animal literature (Cardinal, Pennicott, Sugathapala, Robbins, & Everitt, 2001; Izawa, Zachar, Yanagihara, & Matsushima, 2003; Winstanley, Theobald, Cardinal, & Robbins, 2004; but see Kheramin et al., 2003). Given the difficulty in demonstrating long-term delay discounting in animal models, there are likely to be significant differences between the neural substrates of human intertemporal choice behavior and that studied in model organisms. An important bridging approach will be assessing choices over delays similar to that present in animal models (Luhmann et al., 2008; McClure et al., 2007). As an intriguing example, Gregorios-Pippas, Tobler, and Schultz (2009) used a Pavlovian paradigm to assess the value of rewards received after delays of, at maximum, 13.5 seconds. They find activity in the ventral striatum is modified by delay and is slightly better fit by an exponential decay than a hyperbolic function.

Another study that provides a point of comparison for animal models comes from Tanaka and colleagues (Tanaka et al., 2004), who used a state-dependent Markov-chain task to look for the neural correlates of delayed prize choice. Unlike the majority of studies included in this review, these authors looked for neural differences evoked by a participant's choice of an immediate reward compared to a choice that required several small losses prior to winning a

larger prize (i.e., effort/action-related delay, rather than forced waits). This method incorporates temporal delay according to the number of losses before the prize rather than requiring the participant to focus on the delay period, which would increase discounting (Mischel, 1972). Tanaka and colleagues found ventral-dorsal gradients in the striatum and insula according to the duration of temporal delay in the prize being chosen. They hypothesized that this result reflects multiple cortico-basal ganglia networks that each represent value at a different delay. At first consideration, it seems difficult to compare this study with the other studies listed in Table 1. However, because they use a temporal difference (Sutton & Barto, 1998) formulation of delay discounting, there are potential connections to a large body of literature involving learned associations and studies on decision making. Specifically, delay discounting is related to recent neuroscience work positing an actor/critic model of decision making (O'Doherty et al., 2004; Paulus, Feinstein, Tapert, & Liu, 2004; Preusschoff, Bossaerts, & Quartz, 2006; Seymour et al., 2004; Sutton & Barto, 1998). There is also a significant literature on temporal difference learning in animal models (Barto, 1995; Bayer & Glimcher, 2005; Lau & Glimcher, 2008; Morris, Nevet, Arkadir, Vaadia, & Bergman, 2006; Samejima, Ueda, Doya, & Kimura, 2005; Schultz et al., 1997; Seo, Barraclough, & Lee, 2007; Seo & Lee, 2007), providing an additional method for better connecting their work to animal research. Work by Schultz (Schultz et al., 1997) has shown that the dopamine transmitter system is an excellent candidate for implementing these proposed learning models, leading to well motivated hypotheses (Sagvolden, Johansen, Aase, & Russell, 2005; Tripp & Wickens, 2008) that could explain pathological failures of intertemporal choice (e.g., in attention deficit/hyperactivity disorder, ADHD).

Building Links to the Larger Cognitive Neuroscience Literature

The behavioral models of delay discounting described here require a complex set of component processes: representations of value and time, prospective thought and planning for the future, and methods for comparing disparate

events. These component processes, in many cases, are better described within the psychological and cognitive neuroscience literatures than within economic theory.

Consider the evaluation of delay, itself. To explain both temporal discounting and the variety of framing effects described earlier, there must be both representations of time as well as mechanisms for those representations to alter subjective value. Describing these effects will require the incorporation of a larger body of behavioral and neuroscience research on time perception and its underlying mechanisms (Buhusi & Meck, 2005). While a full consideration of time processing is well beyond the scope of this review, there are recent and tentative first steps toward integrating delay discounting with the cognitive neuroscience of timing and prospection. As noted in a previous section, Ersner-Hersfield and colleagues (2008) asked participants to rate the relevance of adjectives to themselves as well as a future version of themselves. They found that delay discounting rates correlated with the amount of activity in the rostral anterior cingulate when evaluating adjectives for themselves versus evaluating the relevance of adjectives for their future selves. They also find an effect of time in the posterior cingulate, noted previously. Incorporating methods of studying time from the broader cognitive neuroscience literature holds promise for differentiating components of the broad network of activations associated with delay discounting studies.

Moreover, a growing body of literature implicates specific clinical disorders (e.g., addiction) that shape how people evaluate rewards available immediately and after delays. While this review focused on nonclinical research as a way of constraining the scope of our survey, future research should incorporate clinical considerations when trying to understand the mechanisms of intertemporal choice. Specifically, effects like symmetric past and future discounting (Bickel, Yi, Kowal, & Gatchalian, 2008), the hidden zero effect (Magen, Dweck, & Gross, 2008), and changes in discounting with drug state history (e.g., Giordano et al., 2002), all suggest novel pieces for the intertemporal choice puzzle.

Neuroeconomic research typically has the virtue of precision in modeling and rigor in methods; research typically involves a large

number of participants and involves thoroughly discussed hypotheses. As we mentioned earlier, this makes economic phenomena excellent targets for neuroimaging studies that can identify components of models and provide neurobiological constraints for further testing. The one potential pitfall of this sort of exchange lies in the use of reverse inference (Poldrack, 2006). Although intertemporal choice involves regions associated both with valuation and with core prospective and self-directed thought, the specific computations supported by these regions remain unknown. Thus, experimental designs should also extend beyond simple economic paradigms to consider additional forms of intertemporal choice to improve both the specificity and generalizability of these results. Despite substantial progress over the past few years, there remain many unexplored avenues for future research.

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