



The neural correlates of temporal reward discounting

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Temporal reward discounting (TD) refers to the decrease in subjective value of a reward when the delay to that reward increases. In recent years, a growing number of studies on the neural correlates of temporal reward discounting have been conducted. This article focuses on functional magnetic resonance imaging (fMRI) studies on TD in humans. First, we describe the different types of tasks (also from behavioral studies) and the dependent variables. Subsequently, we discuss the evidence for three neurobiological models of TD: the dual-systems model, the single-system model and the self-control model. Further, studies in which nontraditional tasks (e.g., with nonmonetary rewards) were used to study TD are reviewed. Finally, we discuss the neural correlates of individual differences in discounting, and its development across the lifespan. We conclude that the evidence for each of the three neurobiological models of TD is mixed, in that all models receive (partial) support, and several studies provide support for multiple models. Because of large differences between studies in task design and analytical approach, it is difficult to draw a firm conclusion regarding which model provides the best explanation of the neural correlates of temporal discounting. We propose that some components of these models can complement each other, and future studies should test the predictions offered by different models against each other. Several future research directions are suggested, including studying the connectivity between brain regions in relation to discounting, and directly comparing the neural mechanisms involved in discounting of monetary and primary rewards. © 2013 John Wiley & Sons, Ltd.

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INTRODUCTION

Many choices that we face in life require us to trade off anticipated benefits and costs of two options at different points in time. Should I spend all my money now, or should I save for the future? Should I watch this movie, or go to the gym? Should I study for my exam two weeks in advance, or should I wait until I have only one day left? Should I eat a cheeseburger for lunch, or a salad? While eating the cheeseburger might be more rewarding in the short run, healthy food choices have greater long-term benefits. Yet, often people prefer the immediately rewarding option over

the option that is more rewarding in the long run. How trade-offs are made in these intertemporal choices has been studied by animal researchers,^{1–8} (behavioral) economists,^{9–13} psychologists and psychiatrists,^{14–17} and, more recently, cognitive neuroscientists.^{10,18} We may view these choices from the perspective of temporal discounting (TD), which assumes that the subjective value of a reward decreases as the delay to its receipt increases^{19–22} (see also Ref 23; but see Ref 24). Thus, in experimental lab settings, TD tasks are often used to measure these preferences.¹⁶ A typical TD task involves choices between a monetary reward that will be delivered immediately (e.g., \$50 today) and a larger monetary reward that will be delivered after a delay (e.g., \$100 in 1 month). TD tasks are often viewed as measures of impulsive choice, in that enhanced preferences for immediate rewards may indicate greater impulsivity^{17,22,25–30} (see also Ref 31).

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Even though TD varies within participants across contexts and is domain-dependent (e.g., Refs 32, 33), emerging evidence suggests that it has features like a personality trait.³⁴

TD tasks have increasingly been used in psychology and neuroscience, possibly because of their high relevance to psychiatric disorders characterized by atypical impulse control, such as substance abuse (see Refs 15, 35–38 for reviews), attention-deficit/hyperactivity disorder (ADHD) (e.g., Refs 39, 40), pathological gambling,^{38,41} obesity,^{42,43} and anorexia nervosa.⁴⁴ In recent years, a growing number of researchers have used functional magnetic resonance imaging (fMRI) to investigate the neural correlates of TD in healthy individuals.^{18,45} In this article, we will provide a critical review of these fMRI studies on TD. This review will be limited to studies with human participants, primarily conducted by researchers from the fields of psychology and cognitive neuroscience (see Ref 46 for a review of studies from the field of neuroeconomics). Additionally, this article focuses only on studies in which TD tasks were administered, and in which both the delay preceding the large reward and the magnitude of either the immediate or delayed rewards were systematically varied. Studies in which comparable tasks were used that did not meet these criteria were not included in this review (e.g., Ref 47–49). First, we will review different types of TD tasks (also from behavioral studies) and the dependent variables of these tasks. Subsequently, we will discuss the findings of studies in which the neural mechanisms underlying the discounting of monetary rewards were examined. Three different neurobiological models have been proposed to account for the neural correlates of TD. We will describe these models and report evidence that either supports or argues against each of these models. In addition, we will focus

on the neural correlates of discounting as measured with nontraditional tasks, and on neural mechanisms associated with individual differences in TD and its development across the lifespan. Finally, we will suggest future directions for fMRI research on TD.

MEASURING TEMPORAL REWARD DISCOUNTING

In the majority of TD measures, participants are asked to choose between a small reward that is available immediately and a large reward that will be delivered after some delay period. On the basis of participants' preferences in a series of choices between large rewards that are fixed in amount but vary in delay after which they will be delivered and immediate rewards that vary in magnitude but are smaller than the delayed amount, the subjective value of the large reward is determined for each delay duration.^{17,20,50} See for an example Table 1. These values are usually plotted in a graph demonstrating that the subjective value of a reward decreases the longer one has to wait for it. The more the value of the large reward is discounted as a function of time, the steeper the discounting function is (see Figure 1). Steep discounting functions are typically interpreted as a sign of impulsivity^{17,22,25–30} (see also Ref 31).

Types of Tasks

Hypothetical TD tasks with monetary rewards are most commonly used in studies with humans^{51–103} (see Ref 16 for a review). In these tasks, participants make a series of choices between fictional amounts of money, one smaller amount being available immediately and a larger amount available after some specified delay interval. Importantly, participants do

TABLE 1 | Representative Trials and Hypothetical Data of a Temporal Discounting Task with a Fixed Delayed Reward of \$10,000

Amount of Immediate Reward in Dollars	Delay to Large Reward (\$10,000) in Years					
	0	1	2	5	10	20
100	D	D	D	D	D	D
200	D	D	D	D	D	D
500	D	D	D	D	D	I
1000	D	D	D	D	I	I
2000	D	D	D	I	I	I
5000	D	D	I	I	I	I
10,000	D	I	I	I	I	I
Subjective value of delayed reward	10,000	7500	3500	1500	750	350

Preferences for the delayed reward are indicated with a 'D' and preferences for the immediate reward with an 'I'. For each delay, the subjective value of the delayed reward is located where the choice preference switches from delayed to immediate.

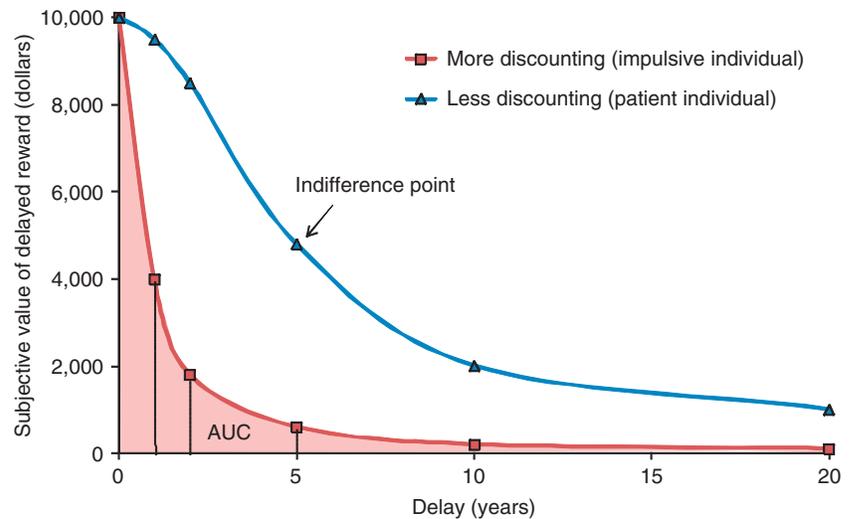


FIGURE 1 | Hypothetical data of a temporal discounting task showing the subjective value of a fixed delayed reward (in this example \$10,000) as a function of its delay to receipt, and showing the area under the curve (AUC, shaded area) for the steep discounting curve.

not endure delays and rewards are not paid. In a typical hypothetical TD task,⁷³ the magnitude of the immediate reward may range between \$1 and \$1000 in steps of \$50, while the delayed reward may be a fixed amount of \$1000 available after a delay ranging from 1 week to 25 years. An example of a choice is between \$500 today and \$1000 after 1 year. Although the money amounts and delay intervals used seem appropriate for human adults, one important limitation of hypothetical tasks is the questionable ecological validity. Presenting a typical hypothetical task as a real task, however, is not feasible, because the money amounts are generally too large to be paid to the participants.

Therefore, some researchers have opted to use *potentially real tasks*, such as Kirby's Monetary Choice Questionnaire.¹⁰⁴ In potentially real tasks, participants are told that one of their choices will be randomly selected and they will be paid according to this one choice.^{9,18,29,44,80,86,105–127} The assumption on which this task design relies is that participants will make all of their choices as though they are real, because they do not know which choice will be selected.

Finally, in *real tasks*, also referred to as *experiential tasks*,¹²⁸ participants experience the consequences of their choices during the experiment: they endure the waiting times and receive the rewards (money amounts displayed on the screen, or coins delivered to the participant). This is a clear advantage in terms of the ecological validity. In real tasks, reward magnitudes are necessarily smaller (typically up to \$1) and delay durations shorter (typically up to 60 seconds) than in hypothetical or potentially real tasks.^{40,128–133} Some of these tasks^{130,131,133} have

proven to be useful in research examining individual differences in children and adolescents.

These hypothetical, potentially real, and real tasks vary greatly in terms of parameter settings. Therefore, one may wonder whether these tasks measure the same construct,^{120,134,135} and whether the same neural circuitries are involved. Hypothetical and potentially real TD tasks yielded similar TD functions,^{80,113,119,120,136} and recruited similar brain regions.¹³⁷ Note, however, that we should be cautious to conclude that any meaningful differences between these two types of discounting are absent based on the lack of statistically significant differences between the hyperbolic discount curves of hypothetical and potentially real tasks (see Ref 138 for an interesting discussion). Hypothetical and real tasks had comparable degrees of discounting,^{113,120,133,139} as long as reward magnitudes and delays were equal.^{114,133,134} Thus, although temporal discounting of small amounts delivered after short delays does not seem to overlap with temporal discounting of large amounts delivered after long delays (which are typically used in hypothetical tasks), task format per se (hypothetical, potentially real, real) may not lead to great differences in discount curves. However, before drawing definite conclusions, more future research is needed in which the overlap and differences between task format within the same sample are studied, including the computation of correlations between discounting rates obtained in different tasks.

TD tasks vary on other factors as well, including: (1) *Types of rewards*. Some studies have used primary rewards such as food, juice, and drugs (hypothetical or real). Hypothetical food and drug rewards are discounted more steeply than hypothetical money.^{58,63,71,84,91,140–152} In terms of real primary

rewards, liquids^{153–156} and erotic pictures^{157,158} have been used. The use of primary rewards in real tasks has the advantage that the reward can be consumed at the end of every trial, unlike money, which cannot be consumed until the end of the task.^{159,160} (2) *The number of different choices*. Some researchers have used tasks in which the magnitude of the immediate reward and the delay to the large reward are kept constant across trials.^{142,161–168} Although the proportion preference for immediate/delayed reward can be computed, the trade-off between reward magnitude and delay duration, as expressed in discounting functions, cannot be measured with these tasks. (3) *Discrete versus continuous choices*. In traditional TD tasks, discrete choices are offered in which the magnitude of the immediate reward and the delay to the large reward is fixed *within* trials. However, in a recently developed task,¹⁶⁹ participants were presented with trials in which the reward/delay ratio rapidly diminished. At any moment during this diminishing ratio, participants could decide whether to quit or continue with the trial. Thus, this task is a more continuous measurement of delay tolerance, offering as a main advantage that ceiling/floor effects can be avoided. (4) *Probability of reward delivery*. In real life, rewards that we receive after a waiting time may be relatively uncertain. In line with this, Reynolds and colleagues^{128,170} found that adolescents rated delayed reward as less certain than immediate rewards, and ratings of uncertainty correlated with degree of discounting. Thus, the use of delayed rewards that are probabilistic may add to the ecological validity of TD tasks.^{48,130,171} This may be implemented optimally in a real task with relatively short waiting times, so that participants can experience the reliability of the delivery of the reward. (5) *The use of delays to the ‘immediate’ reward*. In hypothetical TD tasks, researchers sometimes add an equal delay to both choice options, in order to measure preference reversals. Specifically, in addition to asking participants whether they prefer \$100 today or \$1000 after 12 months (NOW TRIALS), participants may also be asked whether they prefer \$100 after 1 month or \$1000 after 13 months (FUTURE TRIALS). Preference reversals refer to observations that individuals may resist the sooner reward when it is not available immediately, but choose it when it is available right away. This observation has been made in several studies^{40,73,114,135,172–174} and suggests that people’s choices deviate from what would be predicted by economic theory.¹⁷⁵

Dependent Variables

A first step in describing intertemporal choice is to determine the *subjective value* (SV) of the delayed

reward. This value reflects the indifference point for each delay, that is, the choice at which a person has no clear preference for either the delayed reward or the immediate reward. In order to quickly determine an individual’s indifference point, adjusting procedures are often employed. The *adjusting-amount procedure*^{4,29,128,171} uses an online algorithm based on previous choices. If an individual chooses the delayed reward, the amount of the immediate reward is increased on the next trial and vice versa, until the smallest immediate amount chosen over the larger delayed amount is determined. Similarly, the *adjusting-delay procedure*^{125,176} results in increases and decreases of the delay to reward, until the indifference point is reached. Although both methods yielded similar TD functions, the adjusting amount procedure resulted in the most consistent estimates of degree of discounting.¹⁷⁷

When researchers administer a fixed set of trials instead of an adjusting procedure, subjective value can be determined by predetermined rules.^{20,131} Alternatively, it may be determined by fitting a logistic function to the proportion of preferences for the immediate reward, and subsequently determine the monetary amount at which the probability of choosing the immediate reward is 0.5.^{178,179}

When the indifference points (on the *y*-axis) are plotted for all delays (on the *x*-axis), the indifference points are connected with one another, resulting in a discounting curve for each individual. This curve (see Figure 1) can be characterized by different equations: the three most commonly used models are exponential,¹⁷⁵ hyperbolic,^{8,180} and quasihyperbolic ($\beta\text{-}\delta$)¹³ (see Box 1), but also see Ref 138.

Dependent variables include *k*, which governs the degree of discounting (decrease in subjective value; see Box 1), and area under the discounting curve (AUC¹⁸¹; Figure 1). While higher values of *k* indicate relatively steep discounting, larger values of AUC indicate relatively shallow discounting. The main advantage of using AUC is that it is model-free: *k* represents the slope of the discounting curve as estimated with an equation, while AUC is a measure that directly reflects the raw data.¹⁸¹

BOX 1

EXPONENTIAL, HYPERBOLIC, AND QUASIHYPHERBOLIC EQUATIONS

Exponential Equation¹⁷⁵

$$SV = Ae^{-kD},$$

where A is the amount of the future reward, D the delay to its delivery, and k a subject-specific constant that governs the degree of decrease in value, that is, the discount rate.^{182,183}

The exponential equation assumes that a constant change in the delay is associated with the same proportional change in subjective value. Thus, the subjective value of delayed rewards decreases at a constant rate (exponentially) as a function of time.

Quasihyperbolic Equation¹³

$$SV_t = u(c_t) + \beta \sum_{\tau=1}^{\infty} \delta^{\tau} u(c_{t+\tau}),$$

where u is the utility function, c is a consumption, and discount parameters β and δ are between 0 and 1. The discount factor is δ^t for $t=0$, and $\beta\delta^t$ for $t>0$, resulting in a specific weight given to the immediate reward, capturing the present bias.

Hyperbolic Equation^{8,180}

$$SV = A / (1 + kD),$$

where A is the amount of the future reward, D the delay to its delivery, and k a subject-specific constant that governs the degree of decrease in value.^{182,183}

Hyperbolic and quasihyperbolic discount functions are characterized by relatively steep discounting for short-time periods, and by relatively shallow discounting for long-time periods. Thus, as opposed to the exponential equation, both hyperbolic and quasihyperbolic equations can account for preference reversals. Hyperbolic functions have been reported to best fit empirical data.^{182,183}

THE NEURAL BASIS OF TEMPORAL REWARD DISCOUNTING: FMRI RESEARCH

Findings Based on Monetary Tasks

Support for the Dual-System Account

McClure et al.¹²¹ studied the neural basis of preference reversals. In accordance with other dual-systems accounts (e.g., Refs 184–186), they hypothesized that the inconsistency between short-term and long-term preferences is associated with differential activation

of separate and distinguishable neural circuitries. Specifically, they hypothesized that limbic areas such as ventral striatum (VS), ventromedial prefrontal cortex (VMPFC), and posterior cingulate cortex (PCC) mediate the special weight placed on immediate outcomes (β), while lateral prefrontal cortex (LPFC) and associated brain structures mediate a more consistent weighting of delays (δ) (see Box 2, Figures 2 and 3). To this end, they used a potentially real TD task with amounts ranging from \$5 to \$40, and delays ranging from the day of the experiment to 6 weeks later. They included NOW trials and FUTURE trials. The only way in which these trials differed was the presence/absence of an *immediate* reward.

The findings supported their hypotheses (see Box 2) in that (a) deciding during NOW trials as compared to FUTURE trials activated limbic regions (β), i.e., VS, PCC, and medial prefrontal cortex (MPFC). (b) deciding during all choice pairs (NOW and FUTURE) compared with rest activated a δ cluster of regions including intraparietal cortex and dorsolateral prefrontal cortex (DLPFC), ventrolateral prefrontal cortex (VLPFC), and lateral orbitofrontal cortex (LOFC); (c) δ areas were more active than β areas when participants chose the delayed option as compared to the immediate option (see Figure 2). When participants decided not to wait, on the other hand, there was no significant imbalance in activation between δ and β activation (though a trend toward greater β activity was reported). Importantly, these findings remained after controlling for subjective value. The authors interpreted these findings as evidence for competition between two brain systems underlying impulsivity on the one hand and cognitive control on the other.

There is an ongoing discussion as to whether these, and more recent findings, indeed support a dual systems account of TD.^{10,18,45,179,188} Here, we will review recent findings that shed more light on this question (see Table 2). First, in support of McClure et al.,¹²¹ several studies have reported activation in limbic areas during NOW trials versus FUTURE trials, including in VS,^{156,194,198,199} MPFC,^{156,179,194,195,198} and PCC.^{156,179,194,195} One study, however, did not find differences in brain activation between NOW and FUTURE trials.¹⁹⁶ Of note is that the overall supporting evidence was observed despite methodological differences in delay durations and reward magnitudes, nature of the reward (money, juice), trial phase used in analysis (viewing vs deciding), age range, and individual levels of impulsivity. Second, support for the initially found activation in δ areas in response to all trials as compared to rest appears to be more mixed. Although one study¹⁹⁵ reported increased DLPFC and superior

BOX 2

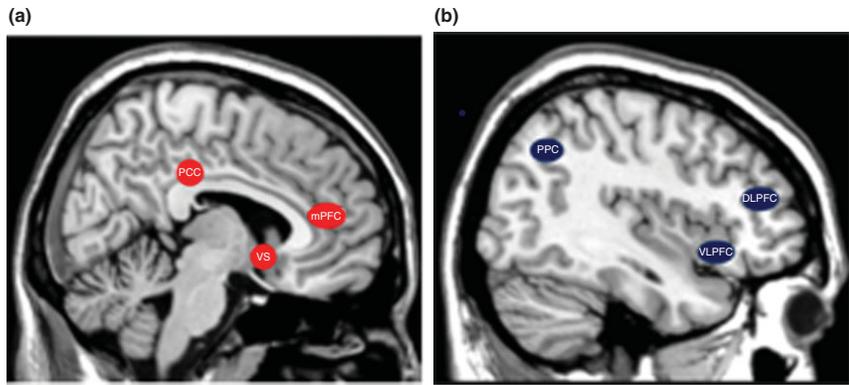
NEURAL ACCOUNTS OF TEMPORAL REWARD DISCOUNTING

In the last decade, there has been a debate about the neural system or systems underlying temporal discounting. In a landmark study, McClure et al.^{121,156} proposed that impulsive preference reversals, that is, being more likely to choose the earlier reward when an immediate reward is present than when both rewards are delayed, reflects the differential activation of two distinguishable neural systems: the limbic ' β ' system, including VS, MPFC, and PCC, which is primarily sensitive to the value of immediate rewards and less sensitive to the value of future rewards, and the more cognitive ' δ ' system, including the LPFC, which is responsive to all types of rewards, whether immediate or delayed, and therefore favors greater rewards even when they are delayed. This led to three specific predictions: (1) NOW trials will preferentially recruit limbic areas as compared to FUTURE trials; (2) NOW and FUTURE trials will trigger activation in δ areas (specifically LPFC) to a similar extent; (3) relatively high levels of LPFC activation are associated with choosing the delayed reward. Recently, this *dual-system account* was challenged by the findings by Kable and Glimcher,^{179,188} who proposed that activity in the VS, MPFC, and PCC tracks the *subjective value* of possible rewards during choice, that is, these brain regions are involved in the valuation of all potential rewards, whether immediate or delayed. Further research in which delays were added to both immediate and delayed rewards, led Kable and Glimcher to refine their *single-system account* into an 'as soon as possible' (ASAP) account, which states that subjective value declines hyperbolically relative to the *soonest* possible reward, rather than to the present. Importantly, the ASAP account does not predict preference reversals. A third account was proposed by Figner et al.²¹² Unlike the single- and dual-system accounts, their *self-control account* suggests that rather than choice following directly from a valuation process of immediate versus delayed rewards, there is an intervening self-control process, subserved by the LPFC (see also Ref 213). Successful self-control can override a prepotent tendency to choose a smaller immediate reward with higher subjective value. The self-control account, therefore, implicates that there can

be a discrepancy between preference expressed by valuation judgments and actual choice. See section *Competing or Complementary Accounts?* of the main text for suggestions as to how model-specific predictions may be tested, and to what extent models may be integrated.

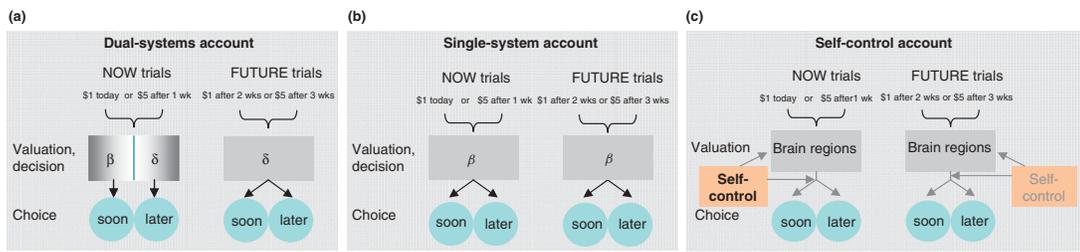
parietal activation during FUTURE trials compared to NOW trials, three other studies reported activation in δ and β regions associated with FUTURE trials,¹⁹⁶ or all trials.^{137,190} While three studies^{121,195,196} used NOW and FUTURE trials, two studies used NOW trials only.^{137,190} The absence of FUTURE trials in these studies may (partly) explain the activation in β areas. Third, when examining differences in activation between δ and β regions when participants chose the delayed option as compared to the immediate one, mixed findings have been reported. One study¹⁹⁶ found that DLPFC activation predicted preferences for delayed rewards, but another study¹⁷⁹ did not find any areas in which activity was greater during preferences for delayed versus immediate rewards. Other studies reported activation associated with the preference for delayed rewards, but not necessarily in δ areas, and even in β areas.^{195,197} Finally, when participants chose the immediate reward as opposed to the delayed reward, one study reported increased activation in VS.¹⁹⁷ This finding is supported by findings of an fMRI study²⁰⁰ which showed that VS activation as measured during reward processing correlated positively with k during a TD task administered outside the scanner. Two other studies failed to identify such β activation.^{196,192} While McClure et al.¹²¹ looked at the interaction between brain areas (δ , β) and choice (immediate, delayed) and found that the difference in activation between δ and β areas was what predicted choice preferences, later studies have only looked at main effects of choice. This makes it difficult to directly compare the findings across studies.

In sum, the majority of support for the notion that there are two separate brain systems that compete while engaging in TD tasks with short-term and long-term choices comes from the reported activation in limbic (β) areas during the viewing of NOW trials versus FUTURE trials. However, less evidence supporting increased activation in δ areas while viewing all choices, or when choosing the delayed reward, is available. Importantly, differences in task designs and specific statistical analyses/contrasts make it hard to draw firm conclusions.



A. β -areas¹¹⁶, or areas involved in valuation of immediate rewards. Note that according to Kable & Glimcher^{174,181}, these areas track the subjective value of all rewards.
 B. δ -areas¹¹⁶, or areas involved in valuation of both immediate and delayed rewards^{174,181}. The DLPFC is a brain region involved in self-control, and plays a pivotal role in the self-control model of temporal discounting²⁰⁴.
 Note. DLPFC = dorsolateral prefrontal cortex, MPFC = medial prefrontal cortex, PCC = posterior cingulate cortex, PPC = posterior parietal cortex, VLPFC = ventrolateral prefrontal cortex, VS = ventral striatum

FIGURE 2 | Brain regions involved in temporal discounting of (monetary) rewards. (a) β -areas,¹¹⁶ or areas involved in valuation of immediate rewards. Note that according to Kable and Glimcher,^{174,181} these areas track the subjective value of all rewards. (b) δ -areas,¹¹⁶ or areas involved in valuation of both immediate and delayed rewards.^{174,181} The DLPFC is a brain region involved in self-control, and plays a pivotal role in the self-control model of temporal discounting.¹⁸⁷



Ad A: Note that β is not displayed for FUTURE trials. Although technically, this system is involved during FUTURE trials, its effect is negligible because it discounts very steeply. Ad C: Note that the influence of LPFC-driven self-control is considered to be especially important during NOW trials, since NOW trials tempt people more than FUTURE trials to choose the soon option.

FIGURE 3 | Visualization of the dual-systems account, the single-system account, and the self-control account. (a) Note that β is not displayed for FUTURE trials. Although technically, this system is involved during FUTURE trials, its effect is negligible because it discounts very steeply.

Support for the Single-System Account

Kable and Glimcher¹⁸⁸ examined whether there are brain regions for which the rate of neural activity is linearly related to the *subjective value* of delayed rewards. For this purpose they designed a potentially real TD task in which participants chose between a fixed immediate reward of \$20 and a larger delayed reward that varied from \$20.25 to \$110, with delays of 6 h up to 180 days. For each trial, they estimated the subjective value of the delayed reward by multiplying the absolute amount of the delayed reward by the discount fraction for that delay, and subsequently used this subjective value as a regressor in their fMRI analysis. They found correlations between *subjective value* and activity in the VS, MPFC, and PCC. Importantly, activity in these regions was better accounted for by subjective value than by either (1) the objective reward amount, (2) the delay to reward, or (3) choice. By showing variation

in activity in these ‘ β ’ regions when the immediate reward was fixed and only the amount of the delayed reward changed, they argued against the dual-systems account (see Box 2, Figure 3). Specifically, the VS, MPFC, and PCC did not exclusively track the value of *immediate* reward, but rather the combination of immediate versus delayed rewards. In a second study, the authors again found that the VS, MPFC, and PCC encoded subjective value, even when the fixed immediate reward was also delayed.¹⁷⁹ Peters and Büchel¹⁹³ also used a fixed immediate reward and replicated the Kable and Glimcher¹⁸⁸ findings.

It should be noted that these studies included individuals who underwent behavioral pretests and were found to have stable discount functions. Individuals with less stable discount functions might show different neural responses.¹⁹¹ Additionally, these participants’ responses appear to be unusual: without preference reversals, and perhaps without exerting

TABLE 2 | Overview of fMRI Studies on Temporal Discounting Providing Evidence for Dual-Systems, Single-System, or Self-Control Account

Study	Participants		Task					Support for Account
	N (female)	Age (years)	Type	Trials (n)	Rewards	Delays	Focus of Analysis	
Ballard and Knutson ¹⁷⁸	16 (8)	M = 21.6	PR	NOW (84)	FIR, VDR	0–6 m	Viewing options	DS/SS/SC
Kable and Glimcher ¹⁸⁸	10 (6)	M = 21.2	PR	NOW (144)	FIR, VDR	6 h–6 m	Viewing options	SS
Kable and Glimcher ¹⁷⁹	25 (13)	M = 22.2	PR	FUT + NOW (200)	FIR, VDR	1 d–6 m	Viewing options	SS
Kim et al. ¹⁸⁹	33 (15)	M = 21.6	HYP	FUT + NOW (?)	VIR, VDR	0–2 m	Decision	DS
Liu and Feng ¹⁹⁰	18 (8)	M = 22	PR	NOW (200)	FIR, VDR	1 d–3 m	Viewing + decision	DS
Luo et al. ¹⁹¹	21 (13)	22–44	PR	NOW (76)	VIR, VDR	4 m	Decision	DS/SS/SC
Marco-Pallares et al. ¹⁹²	17 (11)	M = 28	PR	NOW (104)	VIR, VDR	5–169 d	Decision	SS
McClure et al. ¹²¹	14 (9)	M = 21.4	PR	FUT + NOW (68) ²	VIR, VDR	0–2 m	Decision	DS
Monterosso et al. ⁸⁸	29 (9)	M = 31.8	HYP	NOW (72)	VIR, VDR	1 w–3 m	Decision	—
Peters and Büchel ¹⁹³	22 (14)	M = 26.3	PR	NOW (48)	VIR, VDR	6 h–6 m	Viewing options	SS
Samanez-Larkin et al. ¹⁹⁴	25 (13)	19–26, 63–85	PR	FUT + NOW (84)	VIR, VDR	0–2 m	Decision	DS
Sripada et al. ¹⁹⁵	28 (0)	M = 28.7	PR	FUT + NOW (80)	VIR, VDR	0–2 m	Decision	DS/SS
Weber and Huetzel ¹⁹⁶	23 (11)	19–36	PR	FUT + NOW (130)	VIR, VDR	0–2 m	Decision	SC
Wittmann et al. ¹⁰²	13 (8)	18–39	HYP	NOW (48)	VIR, VDR	5 d–10 y	Decision	—
Wittmann et al. ¹⁹⁷	13 (6)	M = 30.2	R	NOW (21–42)	VIR, FDR	2–64 s	Decision	—

PR, potentially real; FIR, amount of immediate reward fixed; FDR, amount of delayed reward fixed; VDR, amount of delayed reward variable; DS, dual-systems account; SS, single-system account; SC, self-control account; FUT + NOW, future trials (all rewards are delayed) and now trials (choices between an immediate and delayed reward); NOW, only now trials; HYP, hypothetical; VIR, amount of immediate reward variable; R, real; h, hours; s, seconds; d, days; w, weeks; m, months; y, years.

¹Note that only McClure et al.¹²¹ controlled for subjective value in the analyses. Kable and Glimcher¹⁷⁹ tested one prediction from the dual system account, in addition to the predictions from the single system account. Thus, to the best of our knowledge, these studies are the only ones so far which tested predictions of both the single and dual system accounts.

²Estimated on the basis of average task duration and intertrial interval. Note that in some studies, support for the models could not be determined from the results.

much self-control (suggested by the relative lack of activation in δ areas). Another factor to consider is these studies' use of a fixed immediate reward, which is relatively uncommon in the TD literature (see Table 2). According to one report,²⁰¹ rewards are discounted more when the immediate reward is fixed than when the delayed reward is fixed. It is possible that the neural responses in the abovementioned studies also differ from those using fixed delayed rewards (see also Refs 202–207 for other effects of procedural differences on discounting).

Ballard and Knutson,¹⁷⁸ who separated in time the presentation of the *magnitude* of the delayed reward from the presentation of its *delay*, showed that the VS was primarily responsive to magnitude. The MPFC and the PCC, on the other hand, were responsive to both magnitude and delay, which appears in line with the single-system account. This latter finding, however, only occurred in individuals who most often preferred the immediate reward. This implies that the MPFC and PCC might be more sensitive to preference for immediacy than to the value of delayed rewards, in line with the dual-system account.

Two more recent studies^{191,195} found that the VS, MPFC (and PCC) tracked the subjective value of rewards when both the amount of the delayed *and* the immediate reward were variable, lending support to the single-system account. Sripada et al.¹⁹⁵ refined the

earlier findings by Kable and Glimcher, by showing that the *difference* in the subjective value of the delayed versus sooner reward showed this correlation, rather than the sum of the subjective values or the larger subjective value of the two rewards. These studies, however, also show some inconsistencies with the single-system/ASAP account. Sripada et al.,¹⁹⁵ for example, found that the MPFC and PCC were also sensitive to the presence of an immediate reward.

In sum, support for the single system account is provided by studies showing that activation in ' β ' areas is associated with subjective value, even in trials in which an immediate reward is absent. These findings are inconsistent with the dual-systems notion that β regions respond preferentially to immediacy.

Support for the Self-Control Account

Several researchers have proposed that self-control plays a key role in TD,^{14,17,178,186,187,208,209} although support for this notion has been mainly indirect.^{107,178,187,191,210,211} Recently, Figner et al.²¹² provided direct support for the self-control account. In a repetitive transcranial magnetic stimulation (rTMS) study, transient disruption of the left LPFC led to an increase in preferences for immediate rewards. Critically, disruption of this area did *not* lead to changes in the valuation of the choice options. On the basis

of these findings, Figner et al. suggested that preferences for immediate versus delayed reward do not directly result from valuation. Instead, they suggested that even when an immediate reward is valued more highly than a delayed reward, this valuation may be overridden by DLPFC-driven self-control, resulting in the decision to wait for the large delayed reward. Similarly, Cho et al.²¹³ demonstrated that stimulation of the DLPFC led to a *decrease* in the degree of discounting. In line with the above findings, Peper et al.²¹⁴ showed that enhanced structural integrity of PFC-striatum white matter bundles was associated with less impulsive choices. In line with the self-control account, Luo et al.¹⁹¹ argued that brain activation associated with *choice* should be distinguished from brain activation associated with *value*. They found that more difficult choices, reflected by longer reaction times, were associated with greater activation in executive control regions including the inferior frontal gyrus (IFG) and LPFC. Additionally, the DLPFC and IFG were more activated during preferences for delayed rewards compared to immediate rewards, which is in line with the self-control and the dual-system account. Finally, results by Ballard and Knutson¹⁷⁸ also appear to fit the self-control account. For instance, they found that the DLPFC was sensitive to delay, but not to the magnitude of rewards. The authors noted that waiting for a larger future reward requires cognitive control, thereby recruiting regions such as the DLPFC (see Box 2, Figure 3).

Competing or Complementary Accounts?

The dual-systems account, the single-system/ASAP account, and the self-control account may be viewed as competing accounts of the neural basis of TD. We suggest here that (1) the specific predictions of these accounts need to be tested against one another in future research; (2) some components of the accounts may complement each other, and a certain level of integration of the accounts may be possible. We will now discuss each of these points in turn.

(1) To the best of our knowledge, only two studies so far were designed in such a way that some of the predictions of both the single and the dual system accounts could be, more or less directly, tested: McClure et al.¹²¹ controlled for subjective value in the analyses used, and Kable and Glimcher¹⁷⁹ tested one prediction of the dual system account in addition to the predictions of the single-system account. As the use of different tasks might produce differences in both behavior and brain activation, future experiments that test the various accounts directly against each other within a single, specified task, will probably be most useful (see also Ref 215). In order to be able to test all

three TD accounts, such a task should include both NOW and FUTURE trials in which the magnitude of the immediate/sooner reward is varied. Additionally, participants should be asked to complete ratings (using a Visual Analog Scale or a Likert scale) of how they subjectively value the choice options that are used in the task (see Ref 212). These ratings could be used to directly test the predictions of the self-control account against those of the dual- and single-system accounts. If activity in δ areas (specifically LPFC) is associated with the evaluation of choice options *and* with high valuation of delayed rewards, this would support the dual- and single-system accounts. If, on the other hand, LPFC activation is associated with *discrepancies* between choice and valuation (e.g., choosing delayed rewards despite subjective reports that the immediate alternative is higher in attractiveness), then this would be in favor of the self-control account.

The dual-systems and single-system accounts could be tested against each other by combining in one experiment the approaches that were used by McClure et al.¹²¹ and Kable and Glimcher.^{179,188} Specifically, it may be feasible to combine the use of fixed delayed reward trials¹²¹ and fixed immediate reward trials.¹⁸⁸ This would enable one to study whether activity in β areas not only varies as a function of immediacy (NOW vs. FUTURE trials), but also as a function of subjective value and/or delayed reward magnitude. This is relevant, because McClure et al.¹²¹ interpreted the fact that activity in β areas was larger for NOW than for FUTURE trials as evidence supporting the dual systems account. However, these same findings can also be explained by the single system account (activity in β areas reflects the subjective value of rewards at any point in time), because the subjective value of immediate rewards is higher than the subjective value of delayed rewards. Therefore, if future research finds that, within the same group of participants, (1) activity in β areas is larger for NOW than for FUTURE trials, and (2) activity in β areas varies as a function of delayed reward magnitude on fixed immediate reward trials, then that would provide support against the dual system account. If, on the other hand, within the same sample, activity in β areas is stronger for NOW versus FUTURE trials, and there are no regions for which activity is specifically associated with subjective value independent of immediacy/delay, then that would provide support for the dual system account.

(2) Nonetheless, the data of future studies may not provide very clear support in favor of one model and against another. Instead, dual- and single-system accounts might not be mutually exclusive, and integration of both accounts might provide the

best explanation of the data (see also Ref 215). For instance, similar brain regions could be involved in several aspects of TD, such that β -areas correspond to the subjective value of both immediate and delayed rewards (consistent with the single-system account), but that these areas also encode an ‘immediacy signal’ and are therefore more active during NOW trials compared to FUTURE trials (consistent with the dual-systems account). On a similar note, the fact that β areas have been found to primarily respond to subjective value does not exclude the possibility that there are also unique brain areas responding to unique aspects of the choice options, at the same time. To illustrate this, Ballard and Knutson¹⁷⁸ reported findings within the same sample that provided support for both the single system account and the dual-systems account: Both β and δ areas responded to future rewards, but differentially according to delay (δ) and magnitude (β). Similarly, Sripada et al.¹⁹⁵ found that the VS, MPFC, and PCC tracked subjective value (in accordance with the single system account), while the MPFC and PCC were sensitive to the presence of an immediate reward as well (supporting the dual systems account). Luo et al.¹⁹¹ reported a positive correlation between subjective value of the chosen reward and activity in the VS and MPFC. More in line with the dual-systems and self-control account, however, the DLPFC and insula/IFG were more activated during preferences for delayed rewards compared to immediate rewards.

With respect to the self-control account, Figner et al.²¹² primarily view this account as competing with the other two, mainly because in the self-control account, valuation is separated from choice. In the other accounts, on the other hand, choice directly follows from valuation. Additionally, the self-control account is relatively unspecified, both in terms of brain regions involved in the process of valuation, and in terms of the lack of a specific equation which captures the model (see Ref 216 for an *economic* dual-self model of impulse control in which self-control plays a key role). However, we do not want to exclude the possibility that the self-control account may be integrated with the dual- and/or single-system account in the future. But first, more research is needed to further develop the self-control account. Specifically, two important questions include: (1) which brain regions are implicated in valuation? (2) through which specific (neural) mechanisms is LPFC-driven self-control exerted in TD tasks?^{212,213} Regarding the first question, tasks in which rewards are passively experienced, in the absence of overt choice may help to further clarify this.²¹⁷ Regarding the second question, several possibilities have been proposed.^{179,212} One

is the possibility that the LPFC acts as a top-down cognitive control system, overriding valuation, which is computed in other brain regions such as MPFC (see Ref 187). As a result, the delayed reward may be chosen even if it is valued lower than the immediate option. Another possibility is that LPFC does not have a direct effect on choice but rather modulates activity in valuation areas such as MPFC (see Ref 187). In that case, changes in value signal in other areas such as MPFC would mediate the effects of LPFC on choice. For an interesting discussion, see Ref 218.

In sum, data from fMRI studies so far do not provide conclusive evidence in favor of one specific account. Rather, data support all accounts to some extent, and we suggest that integration of the accounts may be feasible. Clearly, future research is needed to refine theoretical accounts of the neural basis of TD.

While this discussion has focused on activation in β and δ areas during TD, other areas have been shown to be active as well (see Box 3).

BOX 3

BRAIN REGIONS THAT MAY NEED FURTHER EXAMINATION

Most reports on temporal discounting mainly focus on the VS, MPFC, and PCC (see Figure 2(a)). Other regions that receive considerable attention, either as part of the ‘ δ ’ system or in relation to subjective value, are the posterior parietal cortex (PPC), LPFC, VLPFC including the IFG (see Figure 2(b)), VMPFC or medial orbitofrontal cortex (MOFC), LOFC, (rostral) anterior cingulate cortex (ACC), and supplementary motor area (SMA). There are, however, other brain regions that have been implicated in TD, but that have received only little attention. These areas include the insula, temporal-parietal junction (TPJ), amygdala, and hippocampus. Activation of the (posterior) insula has been found to correlate with subjective value.¹⁸⁸ The insula has also been found to be more active during choices for delayed rewards,^{102,191} to be activated during both immediate and delayed choices when delays are in the range of seconds,¹⁹⁷ to be part of the ‘ δ ’ system,¹⁹⁴ and to be more active when choices are more risky.¹⁹⁶ Together these results suggest that the insula plays a role in preferences for delayed and uncertain rewards. It should be noted that the anterior and posterior part of the insula might play different roles in TD. Activation of the TPJ was found to correlate with subjective value in one study¹⁸⁸ and to

be inversely related to increasing delays of delayed reward in another study.¹⁷⁸ Just like the insula, the TPJ might, therefore, be part of the ' δ ' system and/or involved in self-control, as with longer delays, activation in this region decreases, which is likely to correspond to a lower subjective value of the delayed reward. Finally, the amygdala and hippocampus have also been implicated in TD, especially when episodic prospection is involved²¹⁹ (see also Findings based on nontraditional tasks). These brain regions have, for example, been found to be more active during choices with a clear preference for either the immediate or delayed reward.¹⁹² Activations in these regions have also been found to correlate with subjective value, and to be more active during choices for later versus earlier rewards.¹⁹⁵ According to McClure et al.,¹²¹ however, the hippocampus is a ' β ' region.

Findings Based on Nontraditional Tasks

In addition to the classical TD tasks that have been discussed, nontraditional TD tasks can shed light on the neural mechanisms of TD. These nontraditional tasks include tasks with primary rewards (juice/food/erotic pictures), tasks in which discounting of future rewards are compared to losses, tasks in which participants envisage a future episode, and tasks in which participants make choices for others instead of themselves (see Table 3).

Although no studies have directly compared the neural correlates of intertemporal choices for primary rewards with secondary rewards, in general, these appear to be quite similar. McClure et al.¹⁵⁶ used juice and water, and found involvement of limbic areas including the VS, MOFC, and PCC during preferences for an immediate reward. Interestingly, in contrast to monetary rewards, only fluid rewards that were delivered immediately elicited this limbic response; a limbic response was not evoked when rewards were delayed by at least 5 min. The authors argued that for primary rewards, the limbic system responds to the *absolute* rather than to the *relative* value of delays. This might be an evolutionary adaptation to physiological needs (e.g., rate of body water loss or deterioration of food). In the case of secondary rewards, the limbic system might be more sensitive to relative value.

When erotic pictures were used, temporal discounting was associated with a similar limbic response.¹⁵⁸ As in studies using monetary reward, Prevost et al.¹⁵⁸ found that activity in the VS and the

VMPFC correlated positively with the subjective value of the delayed reward.

Discounting behavior can also be influenced by using episodic prospection, that is, imagining future episodes such as spending money in a pub 180 days from now,²²⁰ or during a planned vacation in Paris.²¹⁹ Two studies that used episodic prospection found attenuated temporal discounting (i.e., participants were more likely to choose the delayed reward), and this effect was strongest when future episodes were imagined more vividly. At the neural level, Peters and Büchel²¹⁹ found that in both the episodic prospection and the control condition, subjective value correlated with activation in the orbitofrontal cortex (OFC), VS, MPFC, and PCC, although this was not examined by Benoit et al.²²⁰ In addition, Peters and Büchel²¹⁹ reported a pivotal role for the ACC in signaling increased subjective value associated with episodic prospection. Benoit et al.,²²⁰ however, suggested a pivotal role for the more rostrally located Medial rostral prefrontal cortex (mrPFC) in episodic prospection. These discrepant findings may be accounted for by the many differences in task design, including whether participants envisaged the future episode before choosing, the time period and mental process on which the analyses were focused, task format (real vs hypothetical), and the control conditions. Interestingly, both studies found that attenuated discounting was associated with increased coupling of the key medial prefrontal region, that is, the ACC²¹⁹ or the mrPFC,²²⁰ with the hippocampus. According to Peters and Büchel²¹⁹ this increased coupling might reflect increased incorporation of episodic prospection or conceptual information into prefrontal decision-making circuits.

Another interesting question that has been addressed is whether discounting of future losses shares a common neural mechanism with discounting of future gains.^{137,221} The results of these two studies were inconsistent both at the behavioral and the neural level. Xu et al.²²¹ showed that, as predicted, participants were more likely to choose smaller/sooner losses than smaller/sooner gains, but Bickel et al.¹³⁷ found similar degrees of discounting for losses and gains. In line with their behavioral findings, Xu et al.²²¹ showed that the neural mechanisms underlying temporal discounting of gains and losses were asymmetric, that is, greater activation was found in the insula, thalamus, VMPFC, and striatum on loss trials than on gain trials. The PCC and DLPFC were activated in both conditions, but more strongly in the loss condition, suggesting a need for increased cognitive control in order to avoid larger future losses. Bickel et al.,¹³⁷ on the other hand, did not find robust differences

TABLE 3 | Overview of fMRI Studies on Temporal Reward Discounting Using Nontraditional Tasks

Study	Participants		Task				Main Findings
	N (female)	Age (years)	Type	Reward	Trials	Delays	
Albrecht et al. ¹⁹⁸	28 (14)	18–30	PR	Money, playing for self vs. other	80	0–2 m	Steeper discounting and increased activation in VS, anterior MPFC, precuneus, and pregenual ACC when making decisions for self vs other
Benoit et al. ²²⁰	12 (8)	20–36	?	Money, episodic prospection ¹	52	1 m–1 y	Attenuated discounting in imagine trials, associated with increased mrPFC activation and enhanced mrPFC-hippocampus coupling
Bickel et al. ¹³⁷	30 (21)	20–67	PR + HYP	Money, gains and losses	168	1 w–6 m	No significant difference in discounting of gains and losses, and no significant neural differences
McClure et al. ¹⁵⁶	Exp.1: 20 (12) Exp.2: 14 (6)	? ²	R	Juice and water	36	0–25 min	β and δ areas similar to those identified in previous study using monetary reward ¹²¹
Peters and Büchel ²¹⁹	30 (15)	M = 25.4	PR	Money, episodic prospection ¹	118	6 h–6 m	Attenuated discounting in imagine trials, associated with increased ACC, PCC and lateral parietal cortex activation and enhanced ACC-hippocampus and ACC-amygdala coupling
Prevost et al. ¹⁵⁸	18 (0)	M = 23.1	R	Erotic pictures	240	1.5–9 s	Positive correlation between subjective value and activation in VS, VMPFC and LPFC
Xu et al. ²²¹	20 (10)	22–29	PR	Money, gains and losses	84	2 w–1 m	Steeper discounting in loss trials than gain trials, associated with more activation in DLPFC, PPC, VMPFC, insula, thalamus, and striatum in loss trials compared to gain trials

s, seconds; min, minutes; h, hours; d, days; m, months; y, years.

¹ Imagining spending an amount of money in the future.

² Students, exact age not reported.

between loss and gain trials. More studies are needed to elucidate these discrepant findings. In addition to differences in task design and analysis, differences in mean age might play a role (47¹³⁷ vs 25²²¹).

Finally, Albrecht et al.¹⁹⁸ investigated whether people make the same intertemporal choices for others as they would for themselves. Strong discounters chose the sooner option more often for themselves than they did for others, whereas moderate discounters did not differentiate. When participants made choices only for themselves, more activation was found in the pregenual ACC, VS, anterior MPFC, and precuneus for immediate choices than for delayed choices. These brain regions, therefore, appear primarily involved in choices associated with immediate gratification of one's own needs. The authors conclude that making decisions for others does not involve activation in reward-related brain regions, possibly explaining why strong discounters chose relatively patiently when making decisions for others.

Individual Differences

Temporal discounting of rewards is highly variable across individuals, in that some are willing and able to wait 365 days for a reward of \$100, while others do not wait 2 days for the same reward. Neural correlates of individual differences in discounting have been examined by correlating brain activation during decision-making with either self-report measures of impulsivity, or with discounting measures obtained from TD task choices (e.g., k). To ensure large variability in impulsive behavior, some of these studies have included participants who show pathological forms of impulsivity,^{88,222,223} but note that clinical case-control comparisons are omitted from this review.

McClure et al.¹²¹ proposed that activation in limbic (β) areas biases people toward preferring immediate rewards. Therefore, it might be hypothesized that impulsive individuals activate these regions to a greater extent compared to less impulsive people. Nonetheless, evidence for increased recruitment of these areas in highly impulsive subjects is lacking. In contrast, several studies have reported *decreased* activity in the VS and MPFC in more impulsive subjects.^{178,195}

Further, findings regarding the role of δ regions in individual differences in TD have been inconsistent. While some studies have reported *decreased* activation in the lateral PFC, cingulate and parietal cortex in those subjects who were most impulsive,^{88,178} others have found that more impulsive subjects showed *increased* activation in these regions.^{191,223} In addition, Boettiger et al.²²² observed both increased and decreased activation in different putative δ regions

(DLPFC and LOFC, respectively) in more impulsive subjects. Similarly, Wittmann et al.¹⁰² reported both positive and negative correlations between impulsivity and activation in different parts of the IFG, which has been implicated in inhibitory control.

These inconsistent findings could be attributed mainly to the large differences in task design, focus of fMRI analyses and fMRI contrasts between studies. For instance, some authors have compared brain activation during trials in which an immediate reward was present to activation during trials in which all rewards were delayed.¹⁹⁵ Others have focused on activation during specific choices, such as delayed choices¹⁹¹ or difficult choices in which the immediate and delayed reward were close in subjective value.⁸⁸ Moreover, in some studies the focus of analysis has not been on decision-related activity, but rather on activation associated with the processing of magnitude- and delay-related information.¹⁷⁸ Finally, the TD/impulsivity measures that were correlated with brain activation differ strongly between studies as well. The two studies that used self-report measures of impulsivity^{195,223} employed different questionnaires. Most studies have used k as a proxy of TD/impulsivity, but some have used other measures, such as the proportion of immediate choices,²²² or a measure similar to AUC.¹⁰²

In addition to individual differences in impulsivity, two recent studies have focused on other individual differences that might affect TD behavior and brain activation, such as consistency in choices and cultural background. Luo et al.¹⁹¹ investigated whether the degree of consistency (or stochasticity) in intertemporal choices affects the neural mechanisms associated with these choices. They found that inconsistent participants show increased activation in the IFG and insula during delayed choices, compared to more consistent participants. Kim et al.¹⁸⁹ reported cultural differences in TD, both on a behavioral and neural level. American participants discounted delayed rewards more steeply than Korean participants. This behavioral difference was exclusively driven by differences in VS activation between the two groups. In American participants, the VS activated to a greater extent during NOW trials relative to FUTURE trials. The reverse effect was observed in Korean participants, in that they *deactivated* the VS during NOW trials as compared to FUTURE trials. No group differences were observed in the LPFC or PPC. Kim et al.¹⁸⁹ suggested that these behavioral and neural differences could be attributed to the collectivism that is inherent in Eastern cultures, in which impulsive emotions are discouraged because they might negatively influence the goals of the group.

In sum, given the great variability in task designs and analytical approaches between studies, it is difficult to draw a coherent conclusion regarding neural underpinnings of individual differences in temporal discounting of rewards. Taken as a whole, studies clearly implicate both δ and β brain regions. Whether impulsive individuals show heightened or attenuated activation in these regions seems largely dependent on the type of task that is being used, and on the contrasts that are chosen for analyses. Comparison between studies might be further complicated by individual differences in cultural background and consistency of choices of participants, as both factors have been shown to affect discounting behavior and brain activation.

Development of Temporal Reward Discounting

Behavioral studies have shown that the ability to wait for a delayed reward improves linearly with age from childhood to adulthood^{131,152,224,225} (for lifespan development of TD see Refs 73, 226). However, only a handful of fMRI studies on the development of TD have been conducted. In a sample of 12–31-year-old males, Christakou et al.²²⁷ replicated the previously reported linear increase in AUC with age that was observed in behavioral studies. In addition, they showed that the VMPFC was more active during decision-making in individuals who were older and had a greater AUC. In contrast, older age and greater AUC were associated with *decreased* activation in the VS, insula, ACC and parietal cortex during decision-making. Interestingly, increased age and AUC were associated with heightened functional coupling between the VMPFC and VS, and enhanced coupling between the VMPFC and a network of δ regions (e.g., DLPFC, and parietal cortex) during decision-making. Therefore, Christakou et al.²²⁷ concluded that the VMPFC contributes to the development of self-control by regulating reward-related responses in the VS, and by integrating delay-related information from the DLPFC, insula, and parietal cortex. Ripke et al.¹²⁴ used the approach of McClure et al.^{121,156} to compare β - and δ -activation between adolescents (13–15 years) and adults (19–50 years). While adolescents discounted rewards more steeply than adults, activation in β and δ regions was generally similar in both groups. Adults did show more parietal cortex activation than adolescents during decision-making. Greater parietal cortex activity was also related to more consistent choices, and adults were more consistent than adolescents. Therefore, Ripke et al.¹²⁴ speculated that adults compare immediate and

delayed rewards more precisely than adolescents because of increased maturation of the parietal cortex.

Two recent studies^{111,194} included an even wider age range to study the neurocognitive development of TD. These studies used the approach of McClure et al.^{121,156} to compare brain activation between young adults (18–28 years) and older adults (63–85 years). Both studies demonstrated that β and δ activation was largely overlapping in younger and older adults. However, there were also important differences between the studies. Samanez-Larkin et al.¹⁹⁴ did not find a group difference in discounting behavior, whereas Eppinger et al.¹¹¹ reported reduced discounting in older adults relative to young adults. Further, Samanez-Larkin et al.¹⁹⁴ observed that the δ -regressor correlated with activation in VS in older adults, but not in younger adults. Thus, a brain area that is usually considered part of the β network actually contributed to a preference for delayed rewards in older adults. Samanez-Larkin et al.¹⁹⁴ proposed that this activation might reflect older adults' increased experience with receiving delayed rewards. This experience could lead them to anticipate positive emotions during the receipt of a delayed reward. In contrast, Eppinger et al.¹¹¹ found that the δ -regressor correlated with *less* activation in the dorsal striatum in older adults compared to young adults, and that the β -regressor correlated with *less* activation in the VS in older adults. Eppinger et al.¹¹¹ suggested that this attenuated discounting behavior and neural reward sensitivity in older adults could be explained by reduced dopaminergic modulation of the VS with age.

CONCLUSION

In sum, fMRI studies have suggested a variety of brain regions that are involved in the discounting of delayed rewards. These include, but are not limited to, VS, MPFC, PCC, ACC, LPFC, and parietal cortex. According to the dual-systems model, two brain systems (the β -system and δ -system) contribute differentially to the valuation of immediate and delayed rewards. In contrast, the single-system model¹⁸⁸ states that a single network of brain regions tracks the subjective value of both immediate and delayed rewards. A third account posits that self-control processes mediate the valuation of rewards and the eventual choice of a reward, such that even very tempting immediate rewards could be resisted if enough self-control is exerted.

The studies we have reviewed have reported evidence for the dual-systems model,^{121,156,189,194,197–199} the single-system model,^{179,188,193} the self-control model,^{178,191} or multiple models.^{19,178,191,195} We

suggest that some components of these models can also be integrated, and that the specific predictions of each model should be tested against each other in future research. At present, it is difficult to draw a firm conclusion regarding the best neurobiological model of TD, because of large differences in task design and analyses between studies. Here we highlight the most pressing issues for the field.

First, some studies, particularly those that have found (partial) support for the single-system model,^{178,179,188,193} used fixed immediate rewards. When fixed immediate rewards are used (relative to variable immediate rewards), delayed rewards appear to be discounted more steeply,²⁰¹ dissociating the subjective values of the immediate and delayed reward becomes difficult,¹⁹⁵ and a reward prediction error (which activates β -regions) might be induced.¹⁷⁸ Future studies should address these issues. Second, trial types differed between studies, in that many studies followed the approach of McClure et al.^{121,156} by including NOW and FUTURE trials, while others only included NOW trials. Third, some studies^{178,179,188} selected participants who showed highly consistent behavior across several sessions, which is not considered typical in the discounting literature.¹² As one's consistency affects brain activation during intertemporal choices,^{124,191} future research should take the (in)consistency of participants' choices into account. Fourth, some β -regions (i.e., MPFC, PCC, precuneus) show considerable overlap with default mode network regions, which are deactivated during task performance.²²⁸ Thus, some of the β -activity might reflect default mode network activity associated with a decreased need for executive control during NOW trials. This issue could be circumvented by parametrically manipulating the difficulty of NOW trials (see Ref 88). Finally, only McClure et al. examined β - and δ -activity by testing for the *interaction* between choice and brain activation. Additionally, different studies focused on different phases of TD trials in their analyses (viewing the options vs decision-making). Ideally, future studies should measure activation during both phases by using a design in which activity during both phases can be clearly distinguished (e.g., Ref 190).

FUTURE DIRECTIONS

An important future direction is studying functional and structural connectivity between β - and δ -regions in relation to discounting behavior (see Refs 214, 227). Another understudied research question in the current TD literature is the neural mechanisms underlying the development of TD across the lifespan. Future studies should examine within-subject changes in behavioral and neural correlates of TD in children and adolescents using longitudinal designs, or further explore the neurobiological underpinnings of differences in TD between younger and older adults.

It is important to note that individual or age differences in discounting behavior could not only reflect differences in impulsivity, but also differences in other, related processes including subjective time perception^{229,230} and working memory.¹⁴⁰ Similarly, an important issue in developmental TD studies is the fact that participants of different ages might value the same amount of money differently. To address this issue, developmental studies should include a measure of subjective valuation of the rewards that are used in the TD tasks (e.g., likert ratings), and control for age differences in this measure in their analyses (cf. Ref 152). In addition, while an increased preference for delayed rewards is often interpreted as self-control, waiting for a delayed reward can also be considered a risky choice, since with longer delays there is a greater chance that the promised reward will not actually be received.¹⁶ Therefore, future research would benefit from including measures to further elucidate the role such processes play in temporal discounting.

Finally, researchers should be emboldened by the growing number of TD studies which have incorporated nonmonetary or primary rewards in their designs. Primary rewards, while not without complications, offer several advantages over monetary rewards (e.g., immediate consumption of the reward is possible). An exciting new avenue for TD research is the direct comparison of brain mechanisms involved in discounting of monetary and primary rewards.

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