

# The neurobiology of intertemporal choice: insight from imaging and lesion studies

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## Abstract

People are frequently faced with intertemporal choices, i.e., choices differing in the timing of their consequences, preferring smaller rewards available immediately over larger rewards delivered after a delay. The inability to forgo sooner gratification to favor delayed reward (e.g., impulsivity) has been related to several pathological conditions characterized by poor self-control, including drug addiction and obesity. Comparative and functional human studies have implicated a network of brain areas involved in intertemporal choice, including the medial portion of the orbitofrontal cortex (mOFC). Moreover, damage to this cortical area increases preference for immediate gratification in intertemporal decisions. Here, we review recent neuroscientific studies concerning intertemporal choice, suggesting that the mOFC contributes to preference for delayed rewards, either by computing the value of future outcomes (i.e., valuation), or by enabling people to imagine and represent future rewards and their consequences (e.g., prospection).

**Keywords:** impulsivity; intertemporal choice; medial orbitofrontal cortex; prospection; reward; temporal discounting; value.

## Intertemporal choice: an overview

Individuals are often faced with choices whose consequences are spread over time. Such decisions, involving trading off between benefits and costs differing in the time of their occurrence, are commonly defined as intertemporal choices. Making advantageous choices is crucial for survival and adaptation to the environment. People may have to choose, for example, between saving money or spending it immediately, quitting smoking to reduce the risk of future disease or carrying on, remaining home studying for an upcoming exam or enjoying the cinema with friends. In all these cases, the question is: in order to reach the greatest advantage, is it best for

me to indulge in the present or postpone the gain? In taking into account what they prefer and how long they are willing to wait to obtain it, all intertemporal choices affect people's health, wealth and mood (Frederick et al., 2002).

Humans and other animals' preferences for one option over another reflect not just the amount of expected reward, but also the time at which reward will be received. Economic models usually explain this in terms of maximization of achieved utility (Kalenscher and Pennartz, 2008). In order to choose the most rewarding course of action, people consider the utility of the temporally proximal outcome against the utility they assign to a temporally distant outcome. To explore such an issue in the laboratory (both from an economic and psychological point of view), these decisional situations are usually recreated manipulating the amount of the offered rewards (e.g., money for humans), and the time at which these rewards are delivered. As an example, a subject might choose between \$5 now and \$15 in one week.

Economics and psychology have long established that humans and other animals frequently prefer smaller rewards with short-term availability over larger rewards that become available in the long run, even when waiting would yield larger payoffs than pursuing immediate feelings (Ainslie, 1974; Rosati et al., 2007). This phenomenon, known as delay or temporal discounting (Samuelson, 1937; Ainslie, 1975), implies that the subjective value (i.e., utility depending on specific characteristics of a subject) of a potential reward is weakened (discounted), as a function of the time until its delivery (e.g., Myerson and Green, 1995; Cardinal et al., 2001; Kalenscher et al., 2005). In economics, the discounted utility model (Samuelson, 1937) provided, for many years, a theory framework for intertemporal choices, taking into account that all reasons or drives to make such choices can be described by a single parameter, the discount rate (Frederick et al., 2002). Discount rate refers to the subjective value of rewards that decreases by a fixed percentage for each unit of time that those rewards are delayed (Luhmann, 2009). This drop is described, within the discounted utility model, by a curve represented by an exponential function. This model, however, implies that a given temporal delay leads to the same degree of discounting regardless of when it occurs (Loewenstein et al., 2008). For instance, delaying the availability of a reward by one day from now leads to the same degree of discounting of delaying the availability of the same reward by one day from one year (Frederick et al., 2002). More recent research has pointed out that intertemporal behavior may not be linear, and that deviations from rationality in estimating present and future consequences of actions cannot be captured well by an exponential function (Frederick et al., 2002). Both humans and animals care, in fact, more about a delay if it is proximal than if it is

distal in time (Loewenstein et al., 2008), so that reward discounting is initially more prominent, and then, as more time passes, it becomes less steep (Kirby and Marakovic, 1995; Johnson and Bickel, 2008). For instance, one may prefer \$110 in 31 days over \$100 in 30 days, but \$100 now over \$110 tomorrow (Frederick et al., 2002). These so-called 'preference reversals' or 'time inconsistencies' (Frederick et al., 2002) are better explained by a hyperbolic model than by an exponential model, which accounts for non-constant discounting (Mazur, 1987; Cardinal, 2006; Kalenscher and Pennartz, 2008).

Other anomalies in discount rates are detectable when people have to decide, between gains vs. losses, or between small vs. large outcomes. As for the former, losses are usually less discounted in time than are gains: people are eager to receive gains as soon as possible, not so to obtain losses, even if these would be less conspicuous than future losses ('sign effect', Thaler, 1981; Loewenstein, 1987). Second, large quantities of an outcome are discounted less than smaller quantities: larger outcomes are valued more, making people more willing to wait for them ('magnitude effect', Myerson and Green, 1995).

Greater delay discounting in intertemporal choice is usually related to impulsivity (e.g., Takahashi, 2005), that is, an inability to wait for delayed rewards (Takahashi et al., 2007; Frederick et al., 2002). Individuals with higher delay discounting may have impaired self-control (e.g., Takahashi et al., 2007), which is necessary to favor distant important goals over immediate gratification (Shamosh and Gray, 2008). Suboptimal intertemporal choices, indeed, can be observed in conditions characterized by poor self-control, including drug addiction (e.g., heroin or cocaine addiction, cigarette smoking and binge drinking, Bickel et al., 1999, 2007; Vuchinich and Simpson, 1998; Kirby et al., 1999), attention deficit/hyperactivity disorder (Barkley et al., 2001), compulsive gambling (Holt et al., 2003), or obesity (Weller et al., 2008). Substance users (Kirby and Petry, 2004), indeed, show increased discount rates compared to healthy controls, consistent with their inability to make prudent choices forgoing instant gratifying rewards (e.g., drugs) to favor later rewards of larger value (e.g., health). Impaired performance on measures of intelligence, working memory and cognitive abilities are related to both poor self-control and higher delay discounting (Shamosh and Gray, 2008; Shamosh et al., 2008). For instance, it has been observed that children who were able to wait longer to obtain more marshmallows at age 4 or 5 became more academically and socially competent adolescents, rational, planful, and able to deal well with frustration and stress (Mischel et al., 1988), indicating that individual differences in delay gratification are stable in time. Moreover, evidence for a functional relationship between delay discounting and working memory was provided in addicted individuals: neurocognitive training of working memory significantly decreased delay discounting (Bickel et al., 2011).

Large delay discounting rates in adults have been found to correlate with a number of personality traits too, such as extraversion (Ostaszewski, 1996), and a sense of powerlessness over the future (Johnson et al., 2010). However, individual differences in discount rate can be attributable not only to trait

(i.e., differences between subjects, such as genetic factors or personality) but also to internal state features (i.e., differences within the same subject, such as stress or hunger) and aspects of the situation, such as reward type (Kirby 2009; Peters and Büchel, 2011). Indeed, a difference in the ability to resist to immediate gratification can be observed when people are faced with primary or secondary rewards ('domain effect', Frederick et al., 2002). Primary rewards, such as food or drugs and alcohol, due to their perishability, dependence on internal states (e.g., hunger, stress), and desires (Catania, 1998; Odum et al., 2003; Charlton and Fantino, 2008), as well as their ability to rapidly bring to satiety, are discounted at a higher rate than secondary rewards. Compared to primary rewards, money and gift certificates tend to elicit a less strong desire for immediate rewarding consumption (e.g., Odum and Rainaud, 2003; Estle et al., 2007). Metabolism is indeed a powerful determinant of humans' choice of behavior, exerting an effect also on secondary rewards (Wang and Dvorak, 2010): increasing blood glucose levels led to an increase in the value placed on future rewards; vice versa, drinking a beverage without sugar led to an increase in the value placed on current rewards.

Humans have been deemed to be evolutionarily more patient than animals, despite both exhibiting temporal discounting of future delays (e.g., Green and Myerson, 2004; Woolverton et al., 2007). Recently, however, Rosati and colleagues (2007) demonstrated that humans share similar levels of patience with bonobos and chimpanzees in some contexts, for example, when food rewards are at stake. Under some conditions, humans were even less willing to wait for food than chimpanzees. Moreover, Jimura and colleagues (2009) found that, like animals, humans exhibited temporal discounting also with rewards delayed by seconds.

## Functional studies

Why do attempts to resist immediate gratification fail? Recently, neurobiology and cognitive neuroscience have drawn attention to reward-based decision-making (Loewenstein et al., 2008) as the result of complex emotional and cognitive processes, not yet clearly identified. The subjective value (desirability) of a reward is computed in the brain in order for choices to be guided by preferences (Grabenhorst and Rolls, 2009). There is growing evidence that a network of the frontocortical and subcortical brain regions is consistently responsive to rewarding stimuli (e.g., Schultz, 2006; Luhmann, 2009). In humans, the orbital part of the prefrontal cortex (OFC, Schoenbaum et al., 1998, 1999, 2006; Rangel et al., 2008) and its relative medial portion (mOFC) [paralimbic Brodmann's areas (BAs) 25, 13, and medial portion of BA 11, 12 and 10 (Kringelbach and Rolls, 2004; Bechara, 2005)], together with striatal and midbrain areas, such as the entire ventral striatum (including the nucleus accumbens), the medial amygdala, and the substantia nigra (Haber and Knutson, 2010), are thought to play a pivotal role in the reward circuit (Montague and Berns, 2002). Indeed, a large number of studies found that the OFC and the mOFC were activated during anticipation of expected rewards (e.g.,

Mainen and Kepecs, 2009), coding the incentive value of both real and abstract rewards (Damasio, 1994; Rolls et al., 1999; Elliott et al., 2000b; O'Doherty et al., 2001; O'Doherty, 2004; Kringelbach, 2005; Schoenbaum et al., 2006), monitoring the value of different reinforcers (Kringelbach and Rolls, 2004), and responding to changes in outcome predictions (e.g., O'Doherty et al., 2002; Gottfried et al., 2003). Moreover, it has been suggested (Elliott et al., 2000a; O'Doherty et al., 2001; Liu et al., 2007; Mainen and Kepecs, 2009) that the mOFC is specifically sensitive to benefits and positive outcomes, whereas the lateral portion of the OFC is more modulated by costs (i.e., losses or punishments).

More recently, neurobiological research has focused on the neural underpinnings of value encoding of competing rewards, necessary to guide optimal choice behavior among alternatives differing in the time of their consequences. Overall, animal studies suggest a role of the mOFC in intertemporal decision-making (Winstanley et al., 2004). In both rodents (Roesch et al., 2006; Da Costa Araújo et al., 2010) and monkeys (Wallis and Miller, 2003; Padoa-Schioppa and Assad, 2006; Roesch et al., 2006), mOFC neurons were found to encode the subjective value of different foods when choosing between them, and to be sensitive to the reward amount and to the duration of a delay intervening before food delivery, responding more strongly to short delays predicting cues and before larger rewards. Disruption of both rats' (Cardinal et al., 2001; Mobini et al., 2002; Winstanley et al., 2004; Rudebeck et al., 2006) and monkeys' (Tremblay and Schultz, 1999; Izquierdo and Murray, 2004) mOFC was found to alter discount rates, sensitivity (preferences) to size of reward and time to wait for it, and to produce abnormal responses to changes in reward expectations.

In humans, the ventral striatum, mOFC, posterior cingulate cortex, and lateral prefrontal cortex have been identified as other critical neural substrates of intertemporal choices (McClure et al., 2004, 2007; Kable and Glimcher, 2007, 2010). Their specific role, however, is still unclear. Imaging studies by McClure and colleagues (2004, 2007) emphasize the view that discounting behavior reflects the differential activation of two distinguishable neural systems (see also Elster, 1979; Shefrin and Thaler, 1988; Loewenstein, 1996; Loewenstein et al., 2008). One system is responsible for impatient choices, driven by the desire for present outcomes (the 'myopic doer', Thaler and Shefrin, 1981; Elster, 1985, 1986; Graham and Isaac, 2000). The other is responsible for prudent choices, emphasizing more the consequences of choosing delayed outcomes (the 'farsighted planner', Thaler and Shefrin, 1981). These two systems are commonly defined  $\beta$ , the more impulsive system, and  $\delta$ , the more rational system (e.g., Laibson, 1994, 1997; Loewenstein, 1996). On this perspective, the balance between the activation of these two systems is responsible for the impulsivity or the patience exhibited by people during intertemporal choices (e.g., Laibson, 1994, 1997; Loewenstein, 1996; Peters and Büchel, 2011). McClure and colleagues (2004) found that the ventral striatum, mOFC and medial prefrontal cortex were preferentially activated when an immediate monetary option was available, therefore they deemed these structures as the neural bases of the  $\beta$ -system.

Conversely, the lateral prefrontal cortex and the posterior parietal cortex were not preferentially activated by the presence of a particular option, but activated by all types of choice (between immediate vs. delayed options, or between two delayed options), therefore the authors related these areas to the  $\delta$ -system. When the  $\beta$ -system is engaged, it favors the immediate option, whereas when a greater activation in the  $\delta$ -system overcomes that in the  $\beta$ -system, a delayed option is favored (McClure et al., 2004). These activations (McClure et al., 2004) were not found solely using monetary rewards, but also with primary rewards available immediately after each decision (McClure et al., 2007).

Another approach to relate neural activity to intertemporal choices is to link neural states to subjective value directly (Kable and Glimcher 2007, 2010). In the study by Kable and Glimcher (2007), participants were submitted to monetary choices between a fixed option, always immediately available, and a variable option, offered at different delays. Based on behavioral choices, they derived an individual preference curve for each participant, to estimate how the subjective value changed as a function of delay and amount. Brain activity during subsequent intertemporal choices was then examined that covaried with this parameter. It was found that activity in the ventral striatum, medial prefrontal cortex, and posterior cingulate cortex tracked subjective value, regardless of whether the delayed reward could be obtained in hours or in months. Despite marked differences in the discount curves of each subject (ranging from most patient to most impulsive), subjective preferences were mirrored in the pattern of activity in the ventral striatum, medial prefrontal cortex, and posterior cingulate cortex (Kable and Glimcher, 2007). That this activity varied with the delayed option (the immediate option was fixed and never presented on the screen during the experiment) demonstrates that these regions do not value immediate rewards only, but represent the subjective value of delayed rewards (Kable and Glimcher, 2007). According to Kable and Glimcher (2007), therefore, findings from McClure and colleagues (2004) that limbic activity was greatest for immediate rewards, could merely reflect the fact that immediate options generally have a greater subjective value than delayed ones (Kable and Glimcher, 2007).

To strengthen their point further, Kable and Glimcher (2010) conducted a second experiment, including a condition in which two delayed options were offered, testing for preference reversals in the context of a model called 'As Soon As Possible' (ASAP). While the hyperbolic model accounts for a hyperbolic decline of the subjective value with regard to the present, the ASAP model accounts for a hyperbolic decline of the subjective value relative to the soonest possible reward, which may not necessarily be available immediately. The most evident difference between these two models is in the expected occurrence of preference reversals. While McClure and colleagues' (2004, 2007) discounting function predicts that people will sometimes make preference reversals between two delayed options (i.e., choosing the larger later reward, while this same option was previously refused when paired with an immediate one), the ASAP model predicts that people will make the same choice in both conditions, and that

possible changes are just stochastic (Kable and Glimcher, 2010). Indeed, Kable and Glimcher (2010) found that when subjects chose between two delayed options, they were, in some cases, even more impulsive than when an immediate reward was available. At a neural level, the activity in the ventral striatum, medial prefrontal cortex and posterior cingulate cortex was found to track the subjective value of both immediate and delayed rewards. This (absolute) subjective value varied as a function of the delay to the soonest possible reward. Once again, Kable and Glimcher (2010) did not find a greater activation of the ventral striatum, medial prefrontal cortex and posterior cingulate cortex in the immediate condition compared to the delayed condition, showing that these areas do not carry an impulsive signal that primarily values immediate rewards, but rather a value signal for delayed rewards. At any rate, marked differences in the analysis of the above-described studies (McClure et al., 2004, 2007; Kable and Glimcher, 2007, 2010) make a direct comparison of the two diverse findings difficult.

More recently, the study of Ballard and Knutson (2009) provided further evidence for the involvement of the mesolimbic and lateral brain regions in future rewards evaluation, but differentially according to magnitude and delay. Across subjects, activity in the nucleus accumbens, medial prefrontal cortex, and posterior cingulate cortex positively correlated with the magnitude of future rewards, while that in the dorsolateral prefrontal cortex, temporal-parietal junction cortex, and posterior cingulate cortex negatively correlated with the delay of future rewards. Neural activity in response to magnitude and delay was then correlated with discount rates for each participant. More impulsive subjects showed diminished activation of nucleus accumbens to future rewards magnitude (they were even less sensitive to large magnitudes of future rewards), and increased deactivation of dorsolateral prefrontal and parietal cortices to future rewards (Ballard and Knutson, 2009). This functional dissociation is, in fact, reminiscent of the dual-system model of McClure and colleagues (2004, 2007). However, the finding that medial prefrontal cortex and posterior cingulate cortex responded to both immediate and delayed rewards (Ballard and Knutson, 2009) better fits with a unitary model (Kable and Glimcher, 2007, 2010; Peters and Büchel, 2010).

## Lesion studies

Functional neuroimaging studies in humans highlight the role of the mOFC in the evaluation of intertemporal rewards when a choice is required. However, correlational methods cannot demonstrate a causal role for the mOFC during intertemporal decisions. Lesion methods overcome this limitation. Damage to the mOFC in humans results in motivational, emotional, affective and behavioral deficits, such as dysregulated social behavior (Damasio et al., 1991; Damasio and Anderson, 1993), inability to inhibit simple responses, short-term goals preference instead of long-term goals, inability to make advantageous decisions (poor choice pattern), inefficient coping with risk, abolished physiological

responses in anticipation of punishment or before endorsing harmful actions that maximize good consequences (Moretto et al., 2010), all in the presence of well-preserved basic intellectual abilities (Bechara et al., 1997). Moreover, early signs of fronto-temporal dementia (e.g., eating disorders), a pathology affecting also the OFC (Glimcher et al., 2009), may reveal deficits in assigning the correct value to appetitive stimuli (Pasquier and Petit, 1997).

Fellows and Farah (2005) evaluated intertemporal choices in brain-lesioned patients. They compared performance of ventromedial prefrontal cortex patients, dorsolateral frontal patients, in which damage encompassed the frontal cortex but spared the ventromedial prefrontal cortex, non-frontal patients, in which the frontal cortex was spared, and healthy controls. Participants were assessed on intertemporal monetary decisions (Kirby and Marakovic, 1995), and on the 'future time perspective' test, which assesses several facets of future time representation. Ventromedial prefrontal cortex patients showed discounting rates comparable to those of the other two groups of patients and the healthy controls. Concerning 'future time perspective', instead, ventromedial prefrontal cortex patients revealed significantly foreshortened personal future time perspective than healthy controls. These results suggest that despite the fact that the temporal (future) window of ventromedial prefrontal cortex patients was shorter than it was in the other groups, this did not have an impact on intertemporal choice. Fellows and Farah (2005) themselves, anyway, did not exclude the possibility that their discounting task was less sensitive than the future time perspective task. Recent studies have evidenced that focal lesions encompassing the mOFC but not necessarily the ventromedial prefrontal cortex affected temporal discounting in monkeys by increasing its steepness (Rudebeck et al., 2006), which suggest that the mOFC may be the critical region for evaluating different rewards delivered at different times (Noonan et al., 2010). Since in the study by Fellows and Farah (2005) some patients had damage involving the medial prefrontal cortex but sparing the mOFC, their results did not clearly shed light on the role of human mOFC during intertemporal choice.

More recently, Sellitto and colleagues (2010) reconsidered intertemporal choices, comparing mOFC damaged individuals with patients whose lesion spared the frontal lobe, and healthy controls. Precisely, the maximal overlap of lesions in the mOFC was in BAs 10 and 11, and the adjacent medial prefrontal cortex (BA 32). All participants performed three temporal discounting tasks involving, separately, primary (food) and secondary (money and discount voucher). In the three temporal discounting tasks, participants chose between an immediate variable amount of reward and a fixed amount of reward that could be received after a delay (Kirby and Herrnstein, 1995; Myerson et al., 2003; Sellitto et al., 2010). The amount of the immediate reward was adjusted based on the participant's choices, using a staircase procedure that converged on the amount of the immediate reward that was equal, in subjective value, to the delayed reward (Du et al., 2002; Sellitto et al., 2010).

mOFC patients exhibited greater impatience than healthy and brain-damaged control participants across types of

reward. That is, compared to controls, the preference for immediate rewards was increased in mOFC patients, as was the steepness of the hyperbolic function that best described their behavior. Moreover, lesion volume in BA 11 showed a strong correlation with discounting behavior, with larger lesions associated with steep discounting rates. These findings argue for a necessary role for the mOFC in the valuation of rewards, regardless of the type of reward at stake. This is consistent with a recent study (Chib et al., 2009) that found that the ventromedial prefrontal cortex (which includes the mOFC and the medial prefrontal cortex) activity correlated with subjects' value for all types of goods (food, non-food consumable, money), suggesting that a common 'neural currency' (Montague and Berns, 2002), computed via mOFC, underlies the evaluation of different categories of goods.

Interestingly, differences in temporal discounting were observed despite the fact that patients did not rate themselves as impulsive in a self-assessed impulsivity scale (Fossati et al., 2001). This finding confirms previous reports of a lack of awareness and self-insight in ventromedial prefrontal cortex patients (Barrash et al., 2000; Beer et al., 2006; Ciaramelli and Ghatti, 2007; Modirrousta and Fellows, 2008; Sellitto et al., 2010), and stressed the need for converging measures. Moreover, the lesion volume in BA 11 strongly correlated with the discounting behavior, further suggesting that mOFC is a crucial area in evaluating reinforcers. A further, recent study (Figner et al., 2010) focused on the role of cognitive control during intertemporal choices, based on the idea that choice does not follow automatically from valuation, as valuation judgments and choice can be discrepant due to the intervention of deliberative processes. Activity in the lateral prefrontal cortex, often found during intertemporal choices in previous studies (McClure et al., 2004, 2007; Kable and Glimcher, 2007, 2010), is long known to be responsible for the implementation of self-control during several types of task (e.g., Miller and Cohen, 2001; Knoch and Fehr, 2007). When we are faced with tempting short-term gratifications, self-control processes must intervene to resist temptation in favor of a farsighted choice (i.e., the future outcome). Figner and colleagues (2010) described two types of preference reversals: 'self controlled preference reversals', in which, despite the higher valuation of the tempting short-term gratification, the long-term outcome is chosen, and 'impulsive preference reversals', where the long-term outcome has the larger evaluation but the short-term one is chosen. This model predicts more 'self controlled preference reversal' than 'impulsive preference reversal' when self-control mechanisms are normally available. This 'self-control account' (Figner et al., 2010) makes three fundamental predictions. Firstly, the lateral prefrontal cortex is involved in choice but not in explicit evaluation; therefore a virtual disruption of these cortices should affect the former but leave unaltered the latter. Secondly, this disruption should affect, predominantly, choices in which an immediate option is available, not when only delayed options are put against, since the former are strong, tempting and require more self-control. Thirdly, to the extent that disruption of the lateral prefrontal cortex leads to diminished self-control capability, both a reduction in 'self-controlled

preference reversals' and an increase in 'impulsive preference reversals, should be expected. Low-frequency, repetitive, transcranial magnetic stimulation on the lateral prefrontal cortex before performing the choice task resulted in an increase in impatient choices, without changing the pattern of choices involving only future options, or valuation ratings of both types of rewards. These findings support the idea that the lateral prefrontal cortex exerts a modulatory (self-control) role on the activity of regions (e.g., mOFC) involved in intertemporal reward choice (Figner et al., 2010).

Findings of Sellitto and colleagues (2010) have important implications in understanding the mechanisms underlying intertemporal choice, with respect to both the dual vs. unitary model debate (McClure et al., 2004, 2007; Kable and Glimcher, 2007, 2010), and evidence of the lateral prefrontal cortex involvement in intertemporal choices (Figner et al., 2010). According to the dual model (McClure et al., 2004, 2007), during intertemporal choice, the activation of the impulsive  $\beta$ -system, which includes the mOFC, would favor the immediate option, whereas activation of the patient  $\delta$ -system would favor the delayed option (McClure et al., 2004). However, the finding that damage to the mOFC increases impatient choices (Sellitto et al., 2010) does not support the hypothesis that the mOFC underlays the impulsive system (McClure et al., 2004). If this was the case, damage to the mOFC should have resulted in a weak  $\beta$ -system overwhelmed by the  $\delta$ -system, and, consequently, more prudent choices. Rather, the results of Sellitto and colleagues (2010) can be better understood in the context of a unitary model (Kable and Glimcher, 2007, 2010; Peters and Büchel, 2009), according to which the mOFC and adjacent medial prefrontal cortex, ventral striatum, and posterior cingulate cortex, represent the subjective value of both immediate and future rewards, under the top-down modulation of lateral prefrontal cortex (Hare et al., 2009; Figner et al., 2010). Within this network, the mOFC is thought to signal the subjective value of expected outcomes during choice (Rudebeck et al., 2006; Schoenbaum et al., 2006, 2009; Murray et al., 2007; Rushworth et al., 2007; Talmi et al., 2009), by integrating different information (e.g., magnitude, delay; Ballard and Knutson, 2009) coming from different structures (e.g., amygdala, De Martino et al., 2006) into a 'common neural currency', namely, a common scale used to compare future actions and outcomes value (Montague and Berns, 2002).

Sellitto and colleagues (Sellitto et al., 2010; Ciaramelli and di Pellegrino, 2011) proposed two possible mechanisms through which the mOFC may influence valuation and preference of future rewards. On the one hand, the ventromedial prefrontal cortex regions, including the mOFC, are at the core of a network of brain regions involved in self-projection, namely, the ability to shift the perspective to alternatives other than the present (Buckner and Carroll, 2007; Andrews-Hanna et al., 2010). During intertemporal choice, the mOFC may allow individuals to anticipate future experiences associated with rewards, and modulate valuation of future outcomes based on the resulting (positive) affective states (Bechara, 2005). For instance, the mOFC may subserve the ability to imagine and reproduce how we will feel tomorrow after collecting \$15. Moreover, this ability to project the self ahead

in time to pre-experience an event (episodic future thinking, Atance and O'Neill, 2001) was found to be related to temporal discounting. Firstly, individual differences in the differential activation of medial prefrontal regions (including the medial prefrontal cortex and the rostral anterior cingulate cortex) for current vs. future self-relevant information, predicted temporal discounting (Ersner-Hershfield et al., 2009). That is, the degree to which one perceives one's present self as continuous with a future, self predicted the degree to which one was capable to save money for the future: the greater the activation in medial prefrontal regions, the larger the impatience in discounting future rewards (Pronin et al., 2008; Ersner-Hershfield et al., 2009). Moreover, ventromedial prefrontal cortex activity predicted both how much people would enjoy an event in the future, and the extent to which they made impulsive monetary decisions (Mitchell et al., 2010). Secondly, future thinking reduced discount rates, increasing preferences for future outcomes (Benoit et al., 2011; Peters and Büchel, 2011). Hence, damage to the mOFC would lead to a poor representation of future outcomes and, consequently, to shortsighted behavior (Ciaramelli and di Pellegrino, 2011). As a consequence, mOFC patients are unable to envision future rewards, which would be underpowered to compete with salient, current rewards.

On the other hand, the mOFC is the target of top-down signals from lateral prefrontal cortex promoting 'rational' decision-making and self-control, necessary to override more valuable immediate gratification (Christakou et al., 2009; Hare et al., 2009; Figner et al., 2010). The mOFC has been proposed to integrate emotional and cognitive information, enabling more rational behavior (De Martino et al., 2006). Damage to the mOFC, therefore, would prevent lateral prefrontal signals from modulating the value signal influencing preferences, thus depriving patients of self-control during intertemporal decisions. Poor mental time travel and/or poor self-control arguably result in problems anticipating, or adapting behavior to, the long-term consequences of decisions biasing choices towards closer rewards (i.e., 'myopia for the future'; Damasio, 1994, Bechara, 2005; Sellitto et al., 2010; Ciaramelli and di Pellegrino, 2011).

This suggestion is also compatible with a theory of impulse control proposed by Bechara (2005) and Bechara and Van Der Linden (2005), according to which regions in the ventromedial prefrontal cortex, including the mOFC, weight the long-term prospect of a given choice during decision-making (Schoenbaum et al., 2009). In this context, the amygdala is involved in triggering the affective/emotional signals of immediate prospect of pain or pleasure associated with an outcome (impulsive system), whereas the ventromedial prefrontal cortex is involved in triggering emotions from the products of anticipation and future-thinking (reflective system, Bechara, 2004, 2005). The ventromedial prefrontal cortex links two systems together: one, involving the insula and other somatosensory cortices, critical for representing patterns of emotional/affective states; another, involving the dorsolateral prefrontal cortex and the hippocampus, critical for memory and imagination (Damasio, 1994; Bechara, 2004). The imbalance between these competing signals might lead

to the hypervaluation of immediate over future outcomes. The evidence of a biased towards immediate pleasure behavior (reflecting in abnormally steep temporal discounting) in mOFC patients, indeed, is in line with previous evidence that, during the Iowa Gambling Task, mOFC patients made impulsive, 'shortsighted' choices that warranted (monetary) gains in the short-term but proved disadvantageous losses in the long-term (Bechara et al., 1997; Berlin et al., 2004; Anderson et al., 2006).

## Conclusions

Functional neuroimaging and lesion evidence converge to suggest that intertemporal choices, common situations that require trading off between current and anticipated needs, are governed by a network of brain regions, including the mOFC and the lateral prefrontal cortex. In humans, damage to the mOFC leads to steep discounting of future rewards, indicating that this region is necessary either to create vivid representations of future rewards or to integrate the value of competing options during intertemporal decision-making.

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