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Neurobiological bases of intertemporal choices: A comprehensive review☆,☆☆

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ABSTRACT

Intertemporal choices (ICs) are choices that involve trade-off between costs and benefits that take place at different moments in time. The aim of this article is to present a comprehensive literature review on neurobiological bases of IC. We present the functional models of IC and data from neuroimaging studies, namely ALE analysis. With this paper we intended to show the presence of immediate value preference beyond that predicted by a single-parameter exponential discounting model and its mapping to the dual-systems model for brain function. Studies indicate that individuals tend to show inconsistent preferences depending on the time until the rewards are available and support a perspective that intertemporal evaluation reflects neural mechanisms that differ from other forms of choice, although associated value signals are later represented in the context of a common reward system. The IC induces activations in a “nuclear network” and auxiliary areas including inferior prefrontal cortex, medial prefrontal cortex, temporo-parietal cortex, and peri-splenial posterior cingulate. The network of areas sensitive to value is comprised of several regions that include ventral striatum, medial prefrontal cortex, orbitofrontal cortex, and anterior insula. Evidence from neuroimaging and EEG studies corroborates that choices are determined by a dual evaluation system.

Contents

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1. Introduction

Adaptive decision-making facilitates the consumption and distribution of resources in the quest for survival. Some decisions involve choices between two options available immediately that differ in aspects of value (e.g., relative preferences between attributes) or their probability of occurrence (e.g., risk and uncertainty). However, an important class of decisions involves the comparison of options that differ in the time they will be available, such as in choosing between smaller rewards available immediately and larger rewards that can only be obtained after some time. Choices that involve exchanges between costs and benefits that occur at different points in time are defined as intertemporal choices (ICs) (Johnson, 2012; Pimentel, Gonçalves, Scholten, Carvalho, & Correia, 2012).

In this type of IC situations, decision makers must adjust the subjective value of the delayed reward to take into account the waiting time until arrival. Delay discounting (DD) is the process of devaluing results that happen in the future (e.g., Ainslie, 1974; Green & Myerson, 2004; Logue, 1988; Rachlin & Green, 1972), as a means to study IC.

2. Models of intertemporal choices and the Allais Paradox

There is extensive literature on how to model IC behavior. The finding that most individuals willingly sacrifice the value to obtain the reward in a shorter time interval was initially described by Samuelson (1937) and is now replicated and expanded in many studies (Frederick, Loewenstein, & O'Donoghue, 2002; Kalenscher & Pennartz, 2008; Loewenstein & Prelec, 1992; Pimentel et al., 2012). These discounting effects are ubiquitous for both primary rewards (e.g., food, juice; Ainslie, 1974; Kobayashi & Schultz, 2008; McClure, Ericson, Laibson, Loewenstein, & Cohen, 2007; Richards, Mitchell, Wit, & Seiden, 1997) and secondary rewards (e.g., money; Loewenstein & Prelec, 1992; Strotz, 1956; Tesch & Sanfey, 2008; Thaler, 1981). An opposite phenomenon is often observed for repulsive stimuli, which may become more negative if they are located further in time (i.e., increasingly feared; Berns et al., 2006).

2.1. Exponential model

In Samuelson's formula, DD was modeled as an exponential decay function where subjective value (U) after a delay (D) is given by $U = Ae^{-\beta D}$, where A is the amount of reward and β is the discounting rate.

2.2. Hyperbolic model

Newer formulas have adopted alternative mathematical structures to explain irregularities in IC behaviors. Individuals tend to show inconsistent preferences depending on the time until the rewards are available (Prelec & Loewenstein, 1991; Thaler, 1981). For example, when choosing between \$100 now and \$110 in two weeks, most individuals prefer the smaller and more immediate reward. However, when choosing between \$100 in 36 weeks and \$110 in 38 weeks, almost everyone chooses the larger reward — although the delay in this latter scenario is identical to the previous one. This inconsistency, often called the immediacy effect, implies that the mechanism used to compute the intertemporal value shows a strong preference for immediate rewards, but in larger temporal distances the discounting curve becomes smoother (Pimentel et al., 2012). Alternative models that account for these characteristics propose a hyperbolic (Kirby & Marakovic, 1995; Laibson, 1997, 1998; Strotz, 1956) or a quasi-hyperbolic function using two exponential decay functions (Loewenstein, 1996; Phelps & Pollak, 1968; Shefrin & Thaler, 1988).

2.3. Allais Paradox

Although the models described above have proven to be useful, when decisions are made in the face of uncertainty, human attitude toward risk is not consistent (Iqbal, 2013). The classic model of decision under risk is based on the theory of expected utility (Cohen, 2015; von Neumann & Morgenstern, 1944), but the observed behavior of decision-makers is often at odds with the expected utility model. This can be exemplified with the effect that was coined as the Allais Paradox (Allais, 1953).

The Allais Paradox is a well-known bias where the preferences of individuals result in conflicting choices between two identical pairs of options, but with different expected utility and value. Studies have demonstrated that these reversals of preference depend on how the information is presented and described (Harman & Gonzalez, 2015).

In the Allais Paradox, firstly, individuals are typically asked to choose between options A and B and, afterwards, between options C and D (Allais, 1953). For example, individuals have to start by choosing between: (A) \$1 million for sure or (B) a 10% chance of receiving \$5 million, 89% chance of receiving \$1 million, and 1% chance of receiving nothing. Then, individuals have to choose between: (C) 11% chance of receiving \$1 million or (D) 10% chance of receiving \$5 million.

The expected value of option A is \$1 million and the expected value of option B is \$ 1.39 million. According to the expected utility model, individuals are expected to choose the option with the highest expected value, meaning the preference of B over A, and this entails the preference of D over C (Da Silva, Baldo, & Matsushita, 2013). In turn, a preference for A rather than B implies a preference for C instead of D. Nevertheless, individual choices contrast with the predictions of the theory (Koçaslan, 2014). Although showing a preference for D over C, most people choose A in the first set of choices (thus the paradox), and this tendency was labeled as "certainty effect" (Kahneman & Tversky, 1979). Individuals prefer certain options when they are asked to choose between a risky alternative and a certain one. In this scenario, certainty contributes to risk aversion and their decisions become inconsistent between trials.

3. Neurobiological basis of intertemporal choices

It is known that dysfunctions in the mechanisms of IC contribute to a wide variety of anomalies related to decision-making, from inequities in the distribution of resources (Angeletos, Laibson, Repetto, Tobacman, & Weinberg, 2001; Laibson, 1997), to pathologies in which decision-making is altered, such as in addictions (Bickel & Marsch, 2001; Perry & Carroll, 2008), in attention deficit disorders (Critchfield & Kollins, 2001; Plichta et al., 2009), and in antisocial personality disorders (Petry, 2002), among other conditions.

Through a systematic review, Monterosso and Luo (2010) postulate that DD in humans is determined by the competition between two evolutionary brain systems, a more primitive one that discounts delay prematurely, and a more recent one that shows very little discounting. The more recent system comprises sophisticated cognitive functions, such as memory and self-signaling, leading to greater appreciation of subsequent alternatives that are implicit in neocortical structures. These capabilities do not affect choices through competition, but through a process of mediation of primitive and central structures for motivation and reward.

In adults, there are a number of functional neuroimaging studies that shed light on the neural bases of IC. The neurobiological mechanism of IC may be analyzed in two phases: evaluation and choice. As demonstrated in a study by Liu, Feng, Wang, and Li (2012), distinct brain regions seem to be involved in each phase. Specifically, the evaluation phase was associated with the activation of the ventral striatum (VS) and the ventromedial prefrontal cortex (vmPFC). In turn, the processes of choice were associated with the activation of the dorsolateral prefrontal cortex (dlPFC), which is consistent with Monterosso and Luo's thesis (2010) regarding the involvement of a recent brain system in discounting. Thus, the results suggest that dopaminergic mesolimbic regions are sensitive to subjective value during the evaluation phase, though absent in the choice phase.

Recent evolutionary brain regions, such as the medial prefrontal cortex (mPFC), also seem to mediate the impact of priming cues (e.g., brand logos) in the neural encoding of non-related, subjective valuation during temporal decision-making (Murawsk, Harris, Bode, Domínguez, & Egan, 2012). In the study by Murawsk et al. (2012), the preferences of the participants that relied on priming frequently tended toward more immediate rewards during temporal discount tasks — which was associated with modulation of the neural encoding of subjective valuation of choice options in a brain network. It is possible to assume, therefore, a general susceptibility of the decision-making systems to implicit contextual information, and that arbitrary symbols (e.g., brand logos) can be represented as strong stimuli of rewards that may affect decisions.

Even if much is now known on the neural bases of IC, the relationship between discounting models and brain mechanisms remains to be further analyzed.

Kable and Glimcher (2007) presented the hypothesis that the neural systems for evaluation may reflect a singular function of hyperbolic discounting which functions independently from the delay interval (Laibson, 1997; Mazur, 1987; Strotz, 1956). For each participant, they measured the discounting preferences based on independent behavioral sessions, and subsequently matched the results with fMRI data. Kable and Glimcher (2007) concluded that the value of a delayed result was represented in brain regions related to canonical reward, whose activation was consistent with a model of hyperbolic discounting (Glimcher, Kable, & Louie, 2007). Such finding provides evidence that the delay evaluation shares neural mechanisms with other types of evaluation, although important shortcomings can be raised concerning this study and its results (cf. Berns, Laibson, & Loewenstein, 2007; Glimcher et al., 2007). Moreover, different functions do not seem to lead to significantly different results for varying situations of IC, reflecting the general similarity between quasi-hyperbolic and hyperbolic functions.

A possible strategy to disentangle the neural correlates of different models would be to focus the tests on specific intervals of values where higher discrepancies can be predicted. Also, the brain activations that are observed may have upstream or downstream influences on a subjective value representation. As summarized by Tesch and Sanfey (2008), a variety of behavioral effects might modulate the subjective value in IC.

These questions support a central topic for debate in neuroeconomic research: the existence of a common "neural currency" for reward (Deaner, Khera, & Platt, 2005; Montague & Berns, 2002; Montague & King-Casas, 2007). At one extreme, evidence that IC shares evaluation and decision mechanisms with other forms of choice (Benzion, Rapoport, & Yagil, 1989; Green & Myerson, 1996) may support the conclusion that the subjective value is represented by a single neural currency. Therefore, temporal delay is one of the factors that contribute to the representation of the value of a choice option, but said representation of value does not have special qualities due to temporal delay. At the other extreme, evidence of fundamental differences between IC and other types of choice may lead to the conclusion that IC reflects, at least partially, the workings of a separate system for evaluation (Chapman & Weber, 2006; Prelec & Loewenstein, 1991). Therefore, the subjective value of a delayed result will only be compared with other value signals at a final level before the output (e.g., response selection). The current evidence from neuroimaging studies supports an intermediate perspective: that initial aspects of intertemporal evaluation reflect neural mechanisms that differ from other forms of choice, but that associated value signals are later represented in the context of a common reward system (Carter, Meyer, & Huettel, 2010).

4. Brain areas and circuits involved in IC

4.1. Structural neuroimaging

Research on IC using structural neuroimaging is scarce, but a study by Bjork, Momenan, and Hommer (2009), related DD to proportional frontocortical gray matter volumes from 29 healthy adults. Their results demonstrated that dorsolateral and inferolateral frontal cortex gray matter volumes each correlated inversely with preference for immediate gratification during decision making. A study where participants completed a DD questionnaire assessing the extent to which they preferred smaller, immediate rewards to larger, delayed rewards, after undergoing fMRI, revealed a negative correlation between DD and right prefrontal subgyral white matter volume, and a positive correlation with white matter volume in parahippocampus/hippocampus (Yu, 2012).

A more recent study by van den Bos, Rodriguez, Schweitzer, and McClure (2014), using connectivity analyses in both structural and fMRI, explored the relationship between distinct corticostriatal networks involved in IC. Their results showed distinct striatal pathways that were differentially related to DD. Specifically, structural and functional connectivity between striatum and lPFC was associated with increased patience, while connectivity between subcortical areas and striatum was related to increased impulsivity.

Finally, a study that was just published (Tschernegg et al., 2015) examined structural manifestations of trait impulsivity focusing on brain regions associated with DD. Participants underwent fMRI, followed by a DD task outside of the scanner. Results revealed positive correlations between DD and gray matter volume in the striatum, and gray matter volume of the caudate.

4.2. Functional neuroimaging

Evidence from functional neuroimaging is much more profuse, and suggests the existence of a relationship between IC and both subcortical and cortical areas of the reward system. Such studies generally report the activation of the VS, including the nucleus accumbens (NAcc), the mPFC, the dlPFC, as well as the activation of the posterior cingulate cortex (PCC), during DD (Ballard & Knutson, 2009; Kable & Glimcher, 2007; McClure, Laibson, Loewenstein, & Cohen, 2004). For example, Marco-Pallarés, Mohammadi, Samii, and Münte (2010) conducted an fMRI experiment where participants had to decide between a smaller and immediate monetary reward vs. a larger and delayed reward. The results showed two brain networks involved in the decision-making process for immediate and delayed rewards. One network is involved when decisions are made for rewards and delays of equal subjective value, while the other is involved in cases where the value of both the immediate reward and the delay surpasses its alternative. While the posterior medial frontal cortex (PMFC) was the only region that was active in decisions nearing the point of indifference, the network activated by trials with a clear preference for immediate or delayed rewards comprised the vmPFC, ACC, insula, VS, parahippocampal gyrus (PHG), and amygdala. Thus, DD tasks seem to activate a "default network" comprising the frontal pole, the PCC, and also the parahippocampal gyri (Luhmann, Chun, Yi, Lee, & Wang, 2008). This activation suggests that during IC, decision makers simulate the impending delay through a process of prospection (Luhmann et al., 2008).

In a similar approach, Mitchell, Schirmer, Ames, and Gilbert (2010), in two studies using fMRI, demonstrated that individuals display less activity in brain regions associated with introspective self-reference – such as the vmPFC – when predicting how much they would enjoy a future event, than when they predicted their enjoyment of present events. In addition, the extent to which participants made shortsighted monetary decisions several weeks later was predicted by the magnitude of the vmPFC reduction. These findings suggest that shortsighted decisions may result from an inability to imagine the subjective experience of one's future self, as vmPFC is involved in the simulation of future events from a subjective perspective. Hakimi and Hare (2015), using fMRI, examined whether the neural representation of an imagined primary reward predicts the degree to which the value of delayed monetary payments is discounted in a monetary IC task, and they found a correlation between enhanced vmPFC activity during imagined reward and reduced discounting.

Other prefrontal sectors also have important roles in IC. In fact, DD relates to activity in the dlPFC and its connections with the vmPFC. In a study by Hare, Hakimi, and Rangel (2014) it was explored how neural activity relates to individual differences in the discounting of future rewards, during an intertemporal monetary choice task. Their results suggest a similar set of neurobiological mechanisms for tasks that involve delayed gratification in dietary and monetary IC. These authors report increased activity of the left dlPFC when subjects choose the delayed option, typically requiring more self-control. They also found that the connectivity from the left dlPFC to the vmPFC, which is widely associated with the computation of stimulus values (Bartra, McGuire, & Kable, 2013), increased at the time of choice, particularly in trials where the subjects opted for the delayed reward.

Activation in the posterior portion of the dorsomedial prefrontal cortex (dmPFC) seems to be modulated by the value of immediate options, whereas activation in the adjacent anterior dmPFC may be modulated by the subjective value of delayed options (Wang et al., 2014). However, there was also a positive correlation between brain signal change in the ventral mPFC and the “relative value”, in other words, the absolute difference of subjective value between two intertemporal alternatives. Conversely, the activity in the dorsal anterior cingulate cortex showed a negative correlation with the relative value. These findings suggest separate representations of immediate and delayed rewards in the dorsal mPFC, as well as their comparison in the ventral mPFC, to guide decisions. Kable and Glimcher (2007) also found that the VS, the mPFC, and the PCC track the revealed subjective value of delayed monetary rewards.

The functional dissociation of the posterior and anterior dmPFC in the representation of immediate and delayed rewards is congruent with the general architecture of the prefrontal cortex, and may provide a neural basis for the unique human capacities to delay gratification (Wang et al., 2014). The increased activation of dmPFC during IC tasks, together with the lateral prefrontal cortex (lPFC) and the posterior parietal cortex, is being confirmed in recent studies (Rodriguez, Turner, Van Zandt, & McClure, 2015).

One neuroimaging study by Ballard and Knutson (2009) has examined whether distinct neural substrates respond to the magnitude and delay of future rewards. The authors found that activations in the medial prefrontal cortex (mPFC), together with NAcc and posterior cingulate cortex (PCC), positively correlated with future reward magnitude, whereas dlPFC and posterior parietal cortex (PPC) activation negatively correlated with future reward delay. Thus, these results suggest that mesolimbic dopamine projection regions may have higher sensitivity to the magnitude of future rewards, whereas lateral cortical regions may be more sensitive to the delay of future rewards, possibly reconciling distinct neural accounts of DD. Results from a study by Xu, Liang, Wang, Li, & Jiang (2009) regarding the neural mechanisms of DD in a task with a symmetric pattern of gains and losses, also revealed the activation of the lateral prefrontal and posterior parietal areas in the discounting of both future gains and future losses, though their activation was stronger when discounting losses. In fact, the insula, thalamus, and dorsal striatum also evidenced higher activation during IC involving losses, thus suggesting that the enhanced sensitivity to losses may be driven by negative emotions. In addition, there was an activation of the PCC and mPFC when the choices included immediate gains, whereas extra regions including the anterior cingulate cortex (ACC), insula, and superior frontal gyrus were preferentially activated when the choices involved immediate losses. With respect to this, Tanaka, Yamada, Yoneda, and Ohtake (2014) also found that when predicting future losses, there are significant differences in the striatal activity, representing delay length, as well as in insular activity, which represents sensitivity to magnitude. Wittmann, Leland, and Paulus (2007) have already suggested that the posterior insula, which is a critical component of the decision-making neural network, is involved in DD.

It is known that the striatum and its interactions with other cortical and subcortical networks are the basis of reward-based and goal-oriented decisions. Neural activation to shorter delays compared to longer delays was associated with increased activation in the head of the left caudate nucleus and putamen. A study by Wittmann et al. (2007) found that when individuals chose the delayed reward instead of the immediate reward, several brain areas, including the left caudate nucleus, displayed a correlation between discounting and brain activation for the contrast of intervals with delays below 1 year and delays of 1 year or more.

One study compared the behavioral and neural correlates of intertemporal valuation of real and hypothetical monetary gains, as well as hypothetical losses, having been hypothesized that these involve distinct mechanisms (Bickel, Pitcock, Yi, & Angtuaco, 2009). Participants made IC decisions in a gains condition, using both real and hypothetical \$100 money, as well as in a loss condition, using fictive \$100 money. Although no differences were found between levels of discounting across the three conditions, a first analysis of the fMRI data revealed a significant signal change in limbic areas, namely the ACC, striatum, PCC, as well as executive functioning areas, particularly the lPFC, but such effects did not survive after correcting for multiple comparisons. Therefore the congruence of the BOLD signal between real and hypothetical conditions in DD must be further explored.

In order to examine the role of sophisticated cognitive functions, such as working memory (WM) processes in DD, Shamosh et al. (2008) examined DD, intelligence, WM (span tasks, 3-back task), and WM-related neural activity (using fMRI) in a sample of 103 healthy adults. Their results suggested an association between DD and intelligence, partly due to processes instantiated in the anterior prefrontal cortex (aPFC). In addition, the tendency of more intelligent participants to resist smaller, immediate rewards was partially explained by individual differences in the left aPFC (Shamosh et al., 2008). Indeed, activity in the left aPFC was positively associated with WM accuracy and intelligence, and negatively associated with DD, across all subjects. These findings are consistent with the role the prefrontal cortex in executive functioning and its involvement in difficult decisions. In fact, when responding to hard DD trials, participants evidence more activation in areas related to executive functioning, such as the inferior frontal gyrus and the dorsal anterior cingulate cortex, whereas activations of the VS and inferior parietal lobule occur in response to both hard and easy DD decisions (Avsar et al., 2013).

Regarding decisions under uncertainty, delaying the resolution of uncertainty influenced many of the subjects' preferences. It has been argued that choices are modulated by delays because decision makers experience positive or negative utility during the delay interval itself (Luhmann et al., 2008). When outcomes are certain and the outcome is negative, the utility associated with the delay period is referred to as dread (Berns et al., 2006; Berns et al., 2007).

Summing-up, during the processing of gains and losses, there is activation of a broad neural network, comprising the occipital, parietal, and prefrontal cortex, thus suggesting that the same brain structures support different economically relevant behaviors, regardless of the outcome (Faralla et al., 2015). Moreover, two distinct neural circuits were found to be involved in processing immediate and delayed monetary outcomes. Whereas regions of the emotional system, namely, PCC and mPFC, were engaged when an immediate (gain/loss) option was chosen, the occipital cortex and the parietal cortex, in association with the lateral and dlPFC, were activated in delayed choices.

In order to provide a coarse representation of the brain regions consistently involved in DD studies, which seem to show substantial overlapping, Carter et al. (2010) performed an Activation Likelihood

Estimation (ALE) analysis. The ALE is a meta-analysis technique for the analysis of brain imaging studies (Eickhoff et al., 2009; Turkeltaub, Eden, Jones, & Zeffiro, 2002), with several advantages. On the one hand, it identifies areas of activation convergence through several experiments (Turkeltaub, Eickhoff, Laird, Fox, Wiener, & Fox, 2012; van Veluw & Chance, 2014), thus allowing the identification of brain areas consistently activated during different tasks that involve the same neurobiological processes (Cromheeke & Mueller, 2014). On the other hand, this identification provides the necessary empirical support between the studies in favor or against the current theories on the phenomenon to be studied (Gray, 2001; Pessoa, 2008). Wesley and Bickel (2014) also performed an ALE analysis on foci from studies of DD (DD = 449), working memory (WM = 452), finger tapping (FT = 450), and response inhibition (RI = 450). They found that all tasks engaged the activity of the ACC. In specific, FT strongly engaged motor-related brain areas. In addition to motor-related areas, RI engaged frontal brain regions. There was also activation of the right lPFC by RI, DD, and WM, and it was contrasted out of overlap maps. The unique overlap between DD and WM was mostly observed in a functional cluster in the posterior portion of the left lPFC.

Each focus of activation is modeled as a three-dimensional Gaussian probability distribution, where the standard deviation is determined by group size instead of individual time points. The smaller the sample size, the greater the uncertainty (Eickhoff et al., 2009). Activation probability maps are created for each study/experiment, taking into account the maximum probability of activation in each voxel (Belyk & Brown, 2014). These are random-effects analysis tests for the convergence of activations between studies, against a null hypothesis of spatially independent brain activations (Belyk & Brown, 2014).

During the first step, the probabilities of all the activation foci in an experiment are aggregated for each voxel, which is depicted in modeled activation maps (fMRI) or modeled anatomical maps (VBM) (Raschle, Menks, Fehlbaum, Tshomba, & Stadler, 2015). Then, all modeled maps (fMRI and VBM separately) are combined on a voxel-by-voxel basis in order to form an ALE image containing all unthresholded voxel ALE values (Raschle et al., 2015). In the final step, this ALE image is tested against the null hypothesis on the assumption that, regardless of the experiments, all activated voxels are homogeneously distributed in the brain (Raschle et al., 2015). Thus, the null hypothesis model, which is essentially a distribution map created by several permutations of random voxel activation, results from the use of a random-effects statistical method and is tested against the original ALE image according to the chosen significance threshold (Raschle et al., 2015). Therefore, the construction of the null distribution reflects a random special association between different studies. The comparison between the genuine ALE score and this distribution allows for an inference on the convergence among studies, at the same time that it preserves the relationship between individual foci within each study (Raschle et al., 2015). This transition in inference, from fixed or foci-based effects to testing between study effects, allows for a generalization of the results to the entire population of studies from which the analyzed studies were extracted (Raschle et al., 2015).

Carter et al. (2010) performed an ALE analysis of 378 foci in 13 studies using 10,000 permutations (10 mm FWHM), which yielded 25 significant clusters, each representing regions that are more likely to be activated during tasks involving DD. The regions included a network of areas that are known to be sensitive to value, namely VS, mPFC, orbitofrontal cortex, and anterior insula (Gottfried, O'Doherty, & Dolan, 2003; Knutson, Adams, Fong, & Hommer, 2001; Montague & Berns 2002; O'Doherty, Deichmann, Critchley, & Dolan, 2002) or subjective value, namely the PCC (Kable & Glimcher, 2007). A second region is formed by a "nuclear network" of areas (Spreng, Mar., & Kim, 2009) that support prospective processes such as autobiographical memory, theory of mind, and future planning, and include the inferior prefrontal cortex, the mPFC, the temporo-parietal cortex, and the peri-splenial posterior cingulate. Although the list of contrasts included in the ALE analysis is diverse, these two networks were extracted confidently.

4.3. EEG studies

The electrophysiological correlates of intertemporal decision-making were examined in a study by Blackburn, Mason, Hoeksma, Zandstra, and El-Deredy (2012). In this study, the N100/Early Posterior Negativity and the Frontal Related Negativity emerged as event-related potential (ERP) components of interest. Qu, Huang, Wang, and Huang (2013) studied the Feedback Related Negativity (FRN) component of the event related potentials in a simple game task to determine how delayed rewards and losses affect brain activity. The FRN was elicited more negatively only under the conditions of gain in which payment was delayed, as opposed to immediate gain. In this respect, it is possible that DD and the signal effect may be encoded, at an initial evaluation phase, in FRN. Furthermore, LORETA source localization for the FRN component exhibited significantly higher brain electrical activity in the left-fusiform gyrus and right superior temporal gyrus to monetary loss, compared to monetary gain, after incorrect Go/No-Go responses (De Pascalis Varriale, & D'Antuono, 2010).

In a study by Cherniawsky and Holroyd (2013), participants performed a task in which they received both immediate and future rewards and non-rewards. They also completed a DD task without ERP recording. The results showed that immediate, but not future rewards, elicited the reward positivity. High discounters also displayed larger reward positivities to immediate rewards, compared to low discounters, indicating that high discounters relatively overvalued immediate rewards. These results may indicate that high discounters are more motivated to work for monetary rewards than low discounters, regardless of the time of arrival of the incentives.

5. Discussion

FMRI studies tend to report the activation of frontoparietal regions (Kable & Glimcher, 2007), particularly, dmPFC (Rodriguez et al., 2015; Wang et al., 2014), PPC (Ballard & Knutson, 2009; Tanaka et al., 2014; Xu et al., 2009), and lPFC (Bickel et al., 2009), during DD tasks (Ballard & Knutson, 2009; Kable & Glimcher, 2007; McClure et al., 2004). Studies have also demonstrated that, during IC tasks, areas such as the dlPFC (Faralla et al., 2015), ACC (Marco-Pallarés et al., 2010), VS (Kable & Glimcher, 2007; Marco-Pallarés et al., 2010), vmPFC (Hakimi & Hare, 2015; Liu & Feng, 2012; Mitchell et al., 2010), orbitofrontal cortex (Tschernegg et al., 2015), bilateral posterior insular cortex (Wittmann et al., 2007), and prefrontal subgyral (Yu, 2012) show strong activation.

DD is determined by the competition between two evolutionary brain systems: (1) a more primitive one that discounts delay prematurely; and (2) a more recent one that shows very little discounting, comprising sophisticated cognitive functions (e.g., memory and self-signaling) (Monterosso & Luo, 2010). These capabilities do not affect choices through competition, but through a process of mediation of primitive and central structures for motivation and reward.

The neurobiological mechanism of IC may be analyzed in two phases: evaluation and choice, which activate different neural areas (Chapman & Weber, 2006; Prelec & Loewenstein, 1991). The evaluation phase was associated with the activation of the VS and the vmPFC, and the processes of choice were associated with the activation of the dlPFC (Liu et al., 2012). Although, the more recent perspective is an intermediate perspective: initial aspects of intertemporal evaluation reflect neural mechanisms that differ from other forms of choice, but associated value signals are later represented in the context of a common reward system (Carter et al., 2010).

Different neural networks are enabled for immediate or delayed rewards and losses: PMFC was activated on decisions nearing the point of indifference; vmPFC, ACC, insula, VS, PHG, amygdala (Marco-Palarrés et al., 2010) and also PCC and mPFC were activated by immediate (Xu et al., 2009) or delayed rewards (Marco-Pallarés et al., 2010). Activation in dmPFC (Rodirguez et al., 2015; Wang et al., 2014) and lPFC (Rodriguez et al., 2015) seems to be modulated by the value of immediate options. On the other hand, increased activity of the dlPFC is found when subjects choose delayed rewards (Hare et al., 2014). VS, mPFC, and PCC reveal subjective value of delayed monetary rewards (Kable & Glimcher, 2007). Taken together, data suggests that distinct neural substrates respond to magnitude and delay of future rewards. Mesolimbic dopamine projection regions may have higher sensitivity to the magnitude of future rewards (Ballard & Knutson, 2009). When choices involved future losses, the most pronounced activity was observed in the striatum (Tanaka et al., 2014), insula (Tanaka et al., 2014; Xu et al., 2009), ACC, superior frontal gyrus (Xu et al., 2009), left-fusiform gyrus, and right superior temporal gyrus (De Pascalis et al., 2010). Regardless of whether choices involved immediate gains or losses, PCC and mPFC were more activated (Faralla et al., 2015). Concerning delayed choices, occipital cortex, parietal cortex, lateral and dlPFC were activated (Faralla et al., 2015).

Findings also suggested that when subjects imagine the subjective experience of their future self, vmPFC is involved in the simulation of future events from a subjective perspective (Mitchell et al., 2010; Wang et al., 2014). DD tasks seem to activate the frontal pole, PCC, and PHG (Luhmann et al., 2008).

The brain regions that comprise the network of areas sensitive to value include the VS, mPFC, orbitofrontal cortex, and anterior insula (Gottfried et al., 2003; Knutson et al., 2001; Montague & Berns 2002; O'Doherty et al., 2002). On the other hand, the "nuclear network" (Spreng et al., 2009) is composed of regions that include the inferior prefrontal cortex, the mPFC, the temporo-parietal cortex, and the perisplenial posterior cingulate, which also aid prospective processes, such as autobiographical memory, theory of mind, and future planning. Despite the variety of methodologies discussed above and the diversity of the list of contrasts included in the ALE analysis, these two networks can be extracted with confidence.

Neural systems for evaluation may reflect a singular function of hyperbolic discounting (Kable & Glimcher, 2007). The value of a delayed result was represented in brain regions related to canonical reward, whose activation was consistent with a model of hyperbolic discounting (Glimcher et al., 2007; Kable & Glimcher, 2007). Different functions do not seem to lead to significantly different results for varying situations of IC, reflecting the general similarity between quasi-hyperbolic and hyperbolic functions.

The neuronal bases for delay and uncertainty are distinct. In many cases, the preferences of the subjects were influenced by delaying the resolution of uncertainty. Indeed, it has been suggested that delays modulate choices, since decision makers experience positive or negative utility during the delay interval itself (Luhmann et al., 2008). Regarding outcomes that are certain and negative, the utility associated with the delay period is referred to as dread (Berns et al., 2006; Berns et al., 2007), which relates back to the Allais Paradox.

In conclusion, of all the evidence from neuroimaging and EEG studies, the thesis that choices are driven by a dual evaluation system is corroborated.

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