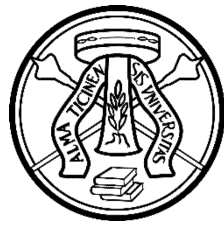


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Now or Later? Exploring the Influence of Interoception and Memory on Delay Discounting

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Abstract

When faced with intertemporal choices – decisions involving tradeoffs between costs and benefits spread over time – humans often forgo better long-term outcomes in favor of immediate rewards, a phenomenon known as delay discounting. Steeper discounting of future rewards is typically associated with impulsive decisions and behaviors commonly observed in pathological conditions such as addiction and obesity. These maladaptive decision-making patterns adversely affect people’s health, prompting researchers into exploring methods for reducing delay discounting. Both interoception and memory-related processes, such as episodic future thinking, have been found to influence delay discounting in both healthy and clinical populations. This thesis aimed to explore the relationship between delay discounting, interoception, and memory. It begins with a general overview of delay discounting and intertemporal choice, including experimental approaches and the neural correlates involved. To establish the influence of interoception and memory on delay discounting, searches were performed across three databases, focusing on articles written in English and involving human participants. The relationships between each concept and delay discounting were further examined within the contexts of obesity and addiction. Evidence suggested that interoception and episodic future thinking are promising targets for reducing delay discounting. However, this thesis also discussed potential shortcomings and discrepancies regarding the results of adopting these approaches, suggesting that combining insights gained from interoception and memory research could be a fruitful strategy for addressing poor delay discounting and its associated maladaptive decisions that negatively impact people’s health, particularly in individuals with obesity and addiction.

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1 Introduction

In 2012, the confectionary brand “Kinder” aired an advertisement called “Curiosity test” on German television. In this commercial, children were presented with a “Kinder® Überraschungs-Ei¹” and were challenged to resist consumption until the adult returned, promising a second egg as a reward. The unfolding scenes depict the children alone in the room, diligently examining and shaking the egg in anticipation, only to ultimately succumb to temptation and indulge in the candy, forsaking the promised yet delayed reward (WerbAll, 2012). This commercial draws inspiration from the Marshmallow test, a psychological experiment wherein children were instructed to choose between obtaining an immediate, less preferred reward or a more desirable one later in time (Mischel et al., 1972). Follow-up research revealed that children displaying the ability to wait for the delayed reward tended to exhibit better life outcomes in adolescence including educational success, self-esteem or stress management (Mischel et al., 1988; Wulfert et al., 2002; but see Watts et al., 2018). Consequently, decision-making as a fundamental element of our everyday life is not only shaping the course of our daily routine but also impacting our future (e.g. deciding between enjoying a slice of cake now or adhering to a healthy diet to fit into the dress for a loved one’s wedding in three months). Such decisions, varying in the timing of their outcomes, are termed **intertemporal choices**. Typically, humans tend to prefer smaller but immediate rewards over larger rewards deferred in time, a phenomenon known as **delay discounting** (Sellitto et al., 2011). Evolutionarily, making ideal decisions was compelling for survival and continues to be so today. The inability to devalue immediate gratification in favor of long-term gain can have implications for health contributing to pathological conditions such as obesity, drug abuse or gambling (Dixon et al., 2003; Sellitto et al., 2011). For instance, pathological gamblers display greater discounting of future monetary

¹ In English: A „Kinder Surprise Egg“ is a hollow egg made of chocolate with a little surprise toy hidden inside.

rewards compared to non-gambling individuals (Dixon et al., 2003). Similarly, compared to normal-weight controls, individuals with obesity selectively exhibit greater preference for immediate food rewards over long-term health benefits, indicating a greater impulsivity in these individuals (Schiff et al., 2016). To mitigate such maladaptive decisions, it is important to understand what processes contribute to the repeated preference of immediate gratification, negatively impacting one's health. In the context of obesity, evidence suggests that preferring immediate food intake over long-term health outcomes is associated with deficits in interoception, related to disordered eating and a higher body mass index (BMI) (Amlung et al., 2016; Martin et al., 2019; Robinson et al., 2021). While impaired interoception is assumed to amplify delay discounting, certain memory processes such as episodic future thinking can decrease delay discounting (Bromberg et al., 2017). Additionally, engaging in retrieval of positive but not negative autobiographical memories can reduce delay discounting, leading to more patient choices (Lempert et al., 2017). Understanding how decision-making, involving different factors, can impact our lives by diminishing the valuation of future rewards or consequences is crucial for promoting future health benefits (Matta et al., 2012). This thesis embarks on delay discounting, one of the cognitive processes underlying decision-making that, if poor or dysregulated, leads to maladaptive health behaviors (e.g. Snider et al., 2020), on the influential role of interoception and memory in decision-making, and the potential interconnections among these three factors.

The following chapters will begin with a brief overview of decision-making, then delve into the realm of intertemporal choice and delay discounting. Furthermore, they will address how interoception and memory-related processes influence delay discounting, with a focus on individuals with obesity and addictions. Finally, I will propose how insights from interoception and memory research on delay discounting could be combined to promote more future-oriented decisions.

2 Shifting concepts in decision-making: Moving beyond the *homo oeconomicus* to embrace the irrational decision-maker

The interest in understanding human decision-making can be traced back to Aristotle's inquiries on practical and deductive reasoning. Despite receiving attention from philosophers for centuries, the examination of decision-making has an extensive history in various disciplines including history, mathematics, and economics to name a few (Buchanan & O'Connell, 2006). Early economic theories of decision-making were concerned with the prediction of an individual's choices and followed two parallel streams examining riskless and risky choices. In the light of riskless choices, the decision-maker was assumed to be a *homo oeconomicus*. The *homo oeconomicus* is characterized by three main features. First, he is completely informed about all possible courses of action and their related consequences. Second, he is infinitely sensitive to different alternatives. Third, the *homo oeconomicus* is rational, meaning that he makes his choices in order to maximize utility (i.e. desirability or satisfaction associated with a particular outcome) (Edwards, 1954).

2.1 Decisions under risk and uncertainty

When it comes to real-life choices, risks and uncertainty are inescapable parts of almost every decision (Loewenstein et al., 2008; Simon, 1959). One example for situations in which risky decisions are made, are games of chance, such as playing a lottery. Mathematically, the best choice is the one to maximize the expected value (i.e. the sum of the product of each possible outcome and its associated probability)²:

$$EV = \sum_i x_i \cdot P(x_i)$$

² Where EV = expected value, $P(x_i)$ = probability of the outcome and x_i = outcome.

Nevertheless, people rarely behave according to the assumption of utility and expected value maximization which can be observed in their behavior. For example, they are inclined to purchase lottery tickets even though the odds of winning are extremely low, and the lottery makes profit from the ticket sales (Edwards, 1954). Therefore, Daniel Bernoulli proposed the **expected utility model** positing that individuals evaluate the potential outcomes of different choices by assigning utility values to those outcomes and then weighing these utilities against the probabilities of their occurrence to determine the overall expected utility of each option. The decision-maker then selects the option that maximizes the expected utility rather than the expected value (Bernoulli, 1896; Loewenstein et al., 2008). This rational choice perspective implies that the decision-maker always chooses the best option among alternatives (Edwards, 1954). The axioms of choice introduced by von Neumann & Morgenstern (1944) provided a framework for modeling rationality and demonstrated that, adhering to these axioms, a decision-maker would behave as proposed by the expected utility model. However, in the middle of the 19th century, experimental psychology was introduced to these economic theories leading to a rapidly increasing number of relevant experiments providing evidence challenging this view (Edwards, 1954; Slovic et al., 1988). Human beings are rather fallible, showing behavioral patterns that are inconsistent with the notion of a homo oeconomicus, thus highlighting the non-perfection of decision-making (Loewenstein et al., 2008). Simon (1956, 1959) limits the ability to make optimal choices by constraining decision-makers to a bounded rationality. According to the author, adaptive models (e.g. learning theories) used in psychology seem to better account for observed decision-making behavior than the economic theories of rational behavior. When adapting, humans do not seek for optimization as proposed by the maximization ideal. Rather, they adapt well enough to the complex and instable environment they are facing when making choices. Alongside environmental features, it is essential to incorporate theories of perceptual and cognitive processes when elucidating decision-making behavior, as they align more closely

with what is observed in both laboratory and field settings (Simon, 1956, 1959). Through the axioms of choice (von Neumann & Morgenstern, 1944) the expected utility model could be empirically tested. Nevertheless, the testing process was based on the assumption that the subjective probabilities assigned to the alternatives by the individual align with the objective probabilities of these outcomes (Simon, 1959). By contrast, Kahneman & Tversky's **prospect theory** (1979) demonstrates that individuals tend to overweight low probabilities while underweighting large probabilities. This suggests that a decision-maker's subjective assessment of a probability may differ from its numerical value (Edwards, 1954). Consequently, the significance of preferences in elucidating human decision-making becomes evident, revealing the limitations of the rational choice perspective. Preferences depend on frames, namely the formulation of decision problems. Changes in framing can cause a shift in preferences that occurs particularly in the loss domain. The authors developed a value function (**Fig. 1**; Tversky & Kahneman, 1991) by which outcomes of risky choices can be evaluated. In general, people tend to display loss aversion, meaning that for them, "losses loom larger than the corresponding gains" (Tversky & Kahneman, 1991, p.1), thus having a greater impact on their preferences (Tversky & Kahneman, 1981, 1991).

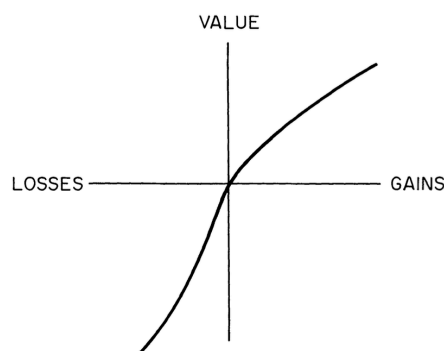


Figure 1. A typical value function depicting losses and gains as value carriers relative to a reference point (Adapted from Tversky & Kahneman, 1991).

The purely cognitive model of Kahneman & Tversky (1979) has been joined over the years by theories capable of expanding this investigation, interweaving them with a linked approach that integrates cognition with the neurophysiological functioning of the nervous system. In this 'bio-psycho-social' perspective, Damasio's **somatic marker hypothesis** (1994) proposes irrational aspects of human behavior by highlighting the crucial influence of emotions in decision-making. Damasio's research involving patients with damage to the ventromedial prefrontal cortex (vmPFC) revealed that these patients exhibited abnormal decision-making, especially in personal and social contexts. Compared to their premorbid state, these patients showed compromised abilities to express emotions and experience feelings, all while retaining intact intellectual and other cognitive functions. Additionally, they made disadvantageous and socially inappropriate choices, resulting in adverse outcomes such as financial losses or a decline in social status (Damasio, 1994; Damasio et al., 1996). Bechara and colleagues (1997) investigated the somatic marker hypothesis in a gambling task that simulated real-life decision-making. Both healthy controls and individuals with vmPFC damage were given a loan of \$2000 and instructed to draw cards from four decks, each containing gains (decks A and B with \$100, decks C and D with \$50) and losses, which were higher in decks A and B compared to C and D. Repeatedly drawing from disadvantageous decks (A and B) resulted in an overall loss while playing the advantageous decks (C and D) led to a net gain. Simultaneously, participants' skin conductance responses (SCRs) were recorded. Healthy controls exhibited anticipatory SCRs before selecting the disadvantageous (i.e. risky) decks after encountering substantial losses, guiding them to avoid these decks. In contrast, vmPFC patients neither avoided the risky decks nor generated anticipatory SCRs, namely somatic markers (Bechara et al., 1997). This underscores the affective processing of different alternatives and their consequences and therefore, another deviation from the expected utility model can be attributed to emotions, particularly the role of somatic markers in decision-making (Loewenstein et al., 2008). The expected utility

model can explain a wide range of phenomena. However, the psychological concepts mentioned above point out the limitations of this classical economic model assuming that human decision-making is solely based on the probability and desirability of outcomes (Loewenstein et al., 2008). Human beings are not perfectly consistent and sensitive, and it is unrealistic to assume that one can be fully informed about every alternative and its consequences, characteristics ascribed to the *homo oeconomicus* (Edwards, 1954). In reality, factors such as uncertainty diminish the expected utility (Frederick et al., 2002). Additionally, each decision-maker's information about the environment is subjective. When non-rational variables arising from cognition, perception, and emotions come into play between the decision-maker and the environment, the rational choice perspective of the expected utility model appears inadequate. Human behavior is more frequently influenced by irrationality, particularly when considering the complex and unpredictable nature of the environment they must navigate. Given these complexities, decision-makers are better represented by the notion of an irrational *adaptive man* rather than adhering to the classical *homo oeconomicus* (Simon, 1959).

Both psychology and economics are interested in understanding human behavior. However, these two disciplines encompass different perspectives of the human being and apply different paradigms to their investigations. Psychology is considered an empirical discipline, formalizing findings only when there is sufficient data to guide the development of theories. By contrast, economics is a more theoretical discipline based on building formal and structured theories. This view comes with a trade-off, as it simplifies assumptions about human behavior not reflecting the complexity of the real world. Nevertheless, the study of decision-making has become a meeting ground for psychology and economics. Alongside exploring the impact of emotions on decision-making (e.g. Damasio, 1994; Loewenstein et al., 2001) and the domain of decision-making under risk, both psychology and economics are also intrigued by the field

of intertemporal choice (Loewenstein et al., 2008), a topic that will be delved into in the upcoming chapter.

3 Intertemporal Choice and Delay Discounting

3.1 Intertemporal Choice

Most decisions people make in their everyday life carry consequences that unfold over time. Choices requiring a trade-off between these temporally dispersed outcomes are conventionally labeled as **intertemporal choices** (Ericson & Laibson, 2019; Matta et al., 2012). Making advantageous choices, which entails demonstrating patience by foregoing immediate rewards in order to attain more valuable future benefits, is essential for both survival and the ability to adapt to one's environment (Rosati et al., 2007; Sellitto et al., 2011). Intertemporal choices are a constant presence in people's lives, whether at work, at home, or during routine activities like shopping, compelling individuals to weigh the consequences of their choices over time (Ericson & Laibson, 2019). Examples abound, such as deciding between studying for an upcoming exam or going on a day trip with friends, choosing whether to splurge on coveted shoes or save the money, or opting for a quick meal from a favorite fast-food restaurant instead of preparing a healthy dinner. In all these cases a consistent pattern becomes evident – there is a need to navigate the trade-off between succumbing to the immediate temptation and postponing gratification for the sake of long-term benefits. Consequently, intertemporal choices impact individuals on a personal level, influencing aspects such as their health, wealth, and happiness (Frederick et al., 2002). Simultaneously, they can play a critical role in addressing broader policy questions such as how to allocate governmental resources (Ericson & Laibson, 2019).

Time preferences are essential not just for theoretical investigations but also constitute an important element in field and laboratory experiments on decision-making (Andreoni et al., 2015). To experimentally examine time preferences, researchers typically employ laboratory samples, using food rewards in animal studies (Ainslie, 1974; Rosati et al., 2007), and monetary rewards for human participants (Andreoni et al., 2015). In these hypothetical decision scenarios,

both the quantity of rewards and the timing of their delivery are commonly manipulated (Sellitto et al., 2011). For example, in Kirby & Herrnstein's experiment (1995), participants were asked to decide between obtaining \$12 in two days or \$16 in 10 days. However, both animals and humans tend to seek immediate gratification even if it entails giving up a larger reward that becomes available later in time (Ericson & Laibson, 2019; Kalenscher & Pennartz, 2008). This phenomenon, referred to as **delay discounting**, is frequently employed in research to explore time preferences in intertemporal choices (Matta et al., 2012) and will be outlined in more detail in the following chapter.

3.2 Delay Discounting

Whenever individuals are confronted with multiple alternatives, they make choices based on their **subjective value**, a process commonly known as value-based decision-making (Rangel et al., 2008). The subjective value reflects an individual's perceived utility or desirability ascribed to a reward and is determined by weighing the benefits and associated costs of a reward, serving as a guiding factor in human choice behavior. This valuation system is subject to modulation by various factors, with one common influence being the delay of the reward delivery (Massar et al., 2015; Rangel et al., 2008). As early as the 19th century, research began examining the factors that account for variations in intertemporal choice behavior, relying on psychological assumptions related to the excitement generated by the anticipation of immediate rewards:

Such pleasures as may now be enjoyed generally awaken a passion strongly prompting to the partaking of them. The actual presence of the immediate object of desire in the mind by exciting the attention, seems to rouse all the faculties, as it were to fix their view on it, and

leads them to a very lively conception of the enjoyments which it offers to their instant possession (Rae, 1834, p. 120).

Later the economist William Stanley Jevons enriched this perspective, acknowledging that having to wait for a reward decreases people's preference for that option:

To secure a maximum of benefit in life, all future events, all future pleasures or pains, should act upon us with the same force as if they were present [...] But no human mind is constituted in this perfect way: a future feeling is always less influential than a present one (Jevons, 1879, p. 78).

Hence, time preferences arise when weighing certain outcomes, favoring the temporally proximal reward over a more distant one, namely delay discounting (Kalenscher & Pennartz, 2008).

3.2.1 Navigating between exponential and hyperbolic functions for modeling Intertemporal Choice behavior

A well-established and predominant framework aimed at capturing time preferences for modeling intertemporal choices is the **discounted utility model** (Samuelson, 1937). This model parallels the expected utility model but employs temporal discount factors instead of probability weights in a weighted sum of utilities (Kalenscher & Pennartz, 2008). The fundamental premise of the model posits that the underlying drives and motives behind time preferences in intertemporal choices can be represented by a single parameter – specifically a **discount rate**. This discount rate can be mathematically modeled using an exponential function (**Fig. 2A**; Kalenscher & Pennartz, 2008; Kirby & Maraković, 1995)³:

³ Where V = present subjective value of a future reward, A = amount of the reward, D = delay to its receipt, and k = discount rate

$$V = Ae^{-kD}$$

Equivalent to the expected utility model, the discounted utility model can be deduced from a set of axioms, one of which assumes a **constant discount rate** (see Koopmans, 1960 for a full review of the axioms). This implies that an individual's subjective value of a reward drops by a consistent percentage for each increment of time those rewards are delayed (Luhmann, 2009). Assuming a constant discount rate suggests that an individual's intertemporal preferences are time-consistent. Time-consistency (i.e. **stationarity axiom**; Koopmans, 1960) posits that an individual's preferences remain unchanged over time, meaning that later preferences align with current or earlier ones. Hence, if a particular reward is ascribed a subjective value higher than another reward at a specific time, it will consistently be assigned a higher value at any other point in time (Frederick et al., 2002; Rangel et al., 2008). Therefore, coupled with the stationarity axiom, a constant discount rate implies that a given delay of a reward has a uniform impact on preferences. Irrespective of the timing of a temporal delay such as whether it is delayed by one week or one year, it results in the same degree of discounting (Frederick et al., 2002; Kallenscher & Pennartz, 2008; Loewenstein et al., 2008). For example, if an individual has the chance to receive \$100 in one year and discounts the future at a rate of 10%, the present value of the amount would be \$90. If the same reward is delayed by two years, one would discount it twice using the same rate of 10%. Graphing the decline in an individual's subjective value of a delayed reward (i.e. a future reward of \$100 being valued at only \$90 in the present) over time reveals an exponentially-shaped curve (Luhmann, 2009).

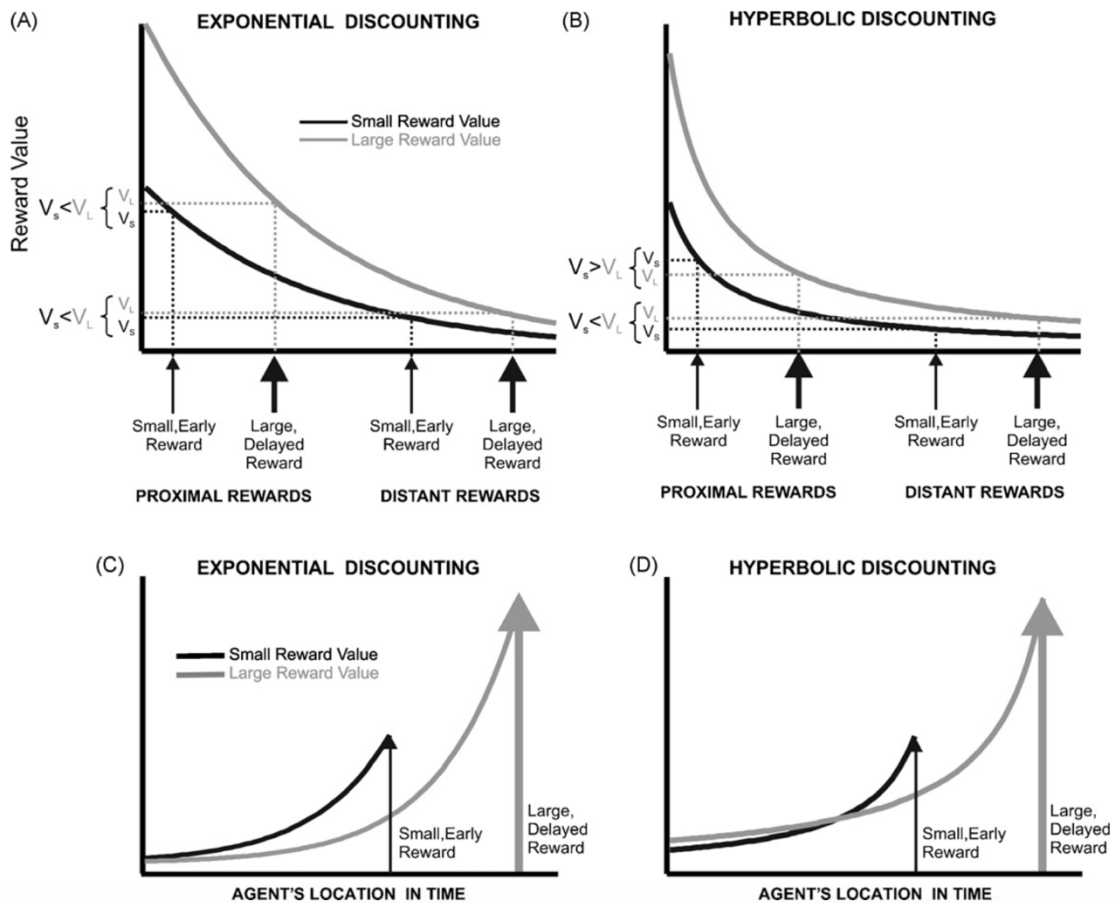


Figure 2. Exemplary exponential and hyperbolic discount functions demonstrating that hyperbolic functions provide a more accurate model for capturing preference reversals. The subject in this example faces a choice between a small, immediate and a large, delayed reward (proximal rewards). Both rewards are then delayed by the same amount of time (distant rewards). In both graphs the y-axis represents the discounted subjective value of a future reward, as a function of the delay to its receipt. The x-axis displays the time delay to the rewards. Black lines represent the small reward's discounted value whereas grey lines represent the value of the larger one. **(A)** In the case of exponential discounting, where a constant discount rate is assumed, the value of the larger, delayed reward (V_L) consistently surpasses the value of the immediate but small reward (V_S), whether they are temporally proximal or deferred by the same amount of time. Hence, $V_S < V_L$ always holds in this scenario. **(B)** Contrastingly, in hyperbolic discounting, the values of the large and small rewards reverse when they are deferred into the future by the same amount of time. Consequently, $V_S > V_L$ when the small and large rewards are temporally proximal, and $V_S < V_L$ when they are distant, indicating a preference reversal for distant rewards. As time progresses, reward discounting becomes less steep. In **(C)** and **(D)** the x-axis indicates the temporal distance to the reward from the subject's perspective, while the y-axis depicts the subjective value. **(C)** The subjective value of the small reward consistently surpasses that of the larger reward, both for proximal and distant rewards. **(D)** The point of intersection represents the preference reversal in hyperbolic discounting. When both rewards are temporally distant (on the left side of the intersection), subjects are expected to favor the larger, delayed reward, as its subjective value exceeds that of the smaller reward. As the time of receipt of the smaller reward approaches (on the right side of the intersection), the subjective value for that reward exceeds that of the larger one, leading the subject to prefer the smaller reward over the larger one (Adapted from Kalenscher & Pennartz, 2008).

Despite its widespread adoption and owing to its simplicity, the discounted utility model has faced challenges from more recent empirical research uncovering various anomalies of the model. This has led to the emergence of alternative frameworks that largely deviate from the once-dominant model of intertemporal choice (Ericson & Laibson, 2019). These approaches often critique the discounted utility model's assumption of exponentiality, particularly the stationarity and the constant discount rate axioms. One common critique relies on the frequent observation of **preference reversals** (Kalenscher & Pennartz, 2008). In a study by Green and colleagues (1994), participants initially favored the smaller immediate monetary reward. However, this preference reversed in favor of the larger, more delayed reward when both rewards were incremented by an equal amount of time. For example, an individual might initially prefer \$20 available now over \$50 available in three months. Yet, this preference might reverse if both rewards are delayed equally (e.g. delayed by one month), leading the individual to prefer \$50 available in four months over \$20 available in one month (Green et al., 1994). These observed time-inconsistencies contradict the stationarity axiom. Instead of remaining preserved, people's preferences between future rewards do change when both rewards are deferred by a fixed amount of time. This phenomenon is also referred to as the '**common difference effect**' or '**immediacy effect**', a specific instance characterized by a noticeable discontinuity in preferences involving immediate rewards (i.e. the sooner option is available right away) (Chapman & Weber, 2006; Kalenscher & Pennartz, 2008). Preference reversals furthermore contradict the constant discounting axiom. Exponential discounting which relies on constant discount rates, assuming that a certain delay has a rigid impact on an individual's subjective value regardless of its timing, fail to capture these preference reversals. There is a high number of empirical evidence suggesting that reward discounting is rather more evident (i.e. steeper) initially and becomes less steep with prolonged delays (e.g. M. W. Johnson & Bickel, 2008; Kirby & Maraković, 1995; Myerson & Green, 1995; Thaler, 1981), which is mathematically best modeled by

a non-constant hyperbolic function (**Fig. 2B**; Kalenscher & Pennartz, 2008; Kirby & Maraković, 1995)⁴:

$$V = \frac{A}{1 + kD}$$

In addition to these deviations from the discounted utility model's assumption of consistent choice, other anomalies have been identified. The so-called '**sign-effect**' (Thaler, 1981) proposes a distinct treatment of gains and losses, with gains being discounted faster than losses. Moreover, the '**magnitude-effect**' reveals that discounting is not amount-independent. Instead, large positive rewards are discounted at a lower rate than small ones (Prelec & Loewenstein, 1991; Thaler, 1981). Finally, '**framing effects**', challenging implications of the expected utility model (Kahneman & Tversky, 1979), are also present in intertemporal choices and can exert an influence on the discount rate. For instance, Faralla and colleagues (2017) used two differently framed decision problems in their experiments. The first one asked participants to choose between immediate and delayed monetary rewards (e.g. receiving €8 now or €11 in one week). In the other decision problem, an explicit penalty was included, indicating a certain amount of money participants would have to sacrifice when deciding for the immediate option (e.g. receiving €11 in one week or €8 now with a penalty of €3). Results revealed preference reversals, with participants favoring the delayed reward when decision frames indicated an explicit penalty (Faralla et al., 2017).

In summary, there is substantial evidence pointing to violations of the theoretical assumptions of the discounted utility model, exemplified by the effects described above (refer to Kalenscher & Pennartz, 2008 for a comprehensive review of other anomalies). These findings suggest that the discounted utility model provides only a limited account to describe

⁴ Where V = present subjective value of a future reward, A = amount of the reward, D = delay to its receipt, and k = discount rate

intertemporal choice behavior. Instances of preference reversals after deferring rewards into the future contradict the assumption of consistent choice and are inadequately explained by exponential models relying on a constant discount rate. Instead, evidence widely supports the use of hyperbolic functions as a more suitable option for modeling the devaluation of rewards over time (i.e. delay discounting) (Kalenscher & Pennartz, 2008).

3.2.2 Investigating Delay Discounting in experimental approaches

Survival necessitates an organism's adaption to its environment. In species with shorter life spans, like rodents, forgoing a present food option in favor of a potentially larger one in the future might not be advantageous. Conversely, species with longer life spans, such as apes, could benefit from postponing immediate gratification. However, discounting of future rewards is observed across several species (Vanderveldt et al., 2016). Notably, delay discounting has been observed in pigeons (Ainslie, 1974), rats (Richards et al., 1997), and in more closer human relatives like chimpanzees and bonobos (Rosati et al., 2007). These evolutionary parallels have provided a useful basis for behavioral research to investigate human choice behavior (Vanderveldt et al., 2016). To understand how people make decisions in daily situations, studying delay discounting is crucial and can be examined through experimental tasks (Matta et al., 2012). While animal studies commonly use primary rewards like food or water (e.g. Richards et al., 1997; Rosati et al., 2007), hypothetical monetary rewards are the predominant choice in experiments examining delay discounting in humans. Typically, subjects are presented with a series of binary choices where they decide between receiving a smaller amount of money available after a very brief delay (or immediately) and receiving a larger amount after a specified delay. Throughout these trials and a given temporal delay, the amount of the rewards can be systematically increased or decreased based on the subject's previous choices, until the subject reports being indifferent in preference, reaching a point known as the **indifference point**. This

point represents the subjective value assigned to the delayed reward. By examining indifference points across various delays for the larger reward, researchers can establish an individual's discount function plotting their subjective value of the larger reward relative to the delay in receiving it (Robles & Vargas, 2008; Vanderveldt et al., 2016). These plotted indifference points constitute the basis that allows researchers to determine the degree of delay discounting. Two widely used measures assess this degree. Firstly, the parameter k is obtained by fitting all subject's indifference points to the hyperbolic discounting model, where a larger k indicates steeper discounting. The other measure involves calculating the **Area Under the Curve** (AUC; Myerson et al., 2001) by summing the areas of the trapezoids formed by plotting the indifference points at each delay. The AUC value ranges from 0 to 1 and, in contrast to k , steeper discounting is associated with lower values of AUC (Odum, 2011a; Odum et al., 2020; Rung et al., 2018; Smith & Hantula, 2008). Among the various techniques utilized to assess delay discounting by identifying subjects' indifference points (Odum et al., 2020)⁵, two commonly employed delay discounting tasks are based on either fixed-alternatives or titrating procedures.

In the **fixed-alternatives task** participants are presented with predetermined hypothetical sums of money and a specific delayed amount (Rung et al., 2018). In Rachlin et al (1991), subjects were instructed to choose between several immediate amounts and a \$1000 delayed reward. The immediate amounts decreased from \$1000 to \$1 across trials, each paired with one of seven delays (1 week, 2 weeks, 1 month, 6 months, 1 year, 5 years, and 25 years). Following the presentation of the list of immediate rewards across all delays, the authors determined participants' indifference points for each delay. This involved averaging the immediate amounts before and at the point of preference reversal, where participants switched from choosing the immediate reward to selecting the delayed one. Furthermore, these indifference points

⁵ e.g. the monetary choice questionnaire (Kirby et al., 1999), fill-in-the-blank (Chapman, 1996), random order survey (e.g. Mitchell, 1999; Robles & Vargas, 2008), visual analogue scale (VAS; e.g. P. S. Johnson et al., 2015), and adjusting-delay (e.g. Koffarnus & Bickel, 2014).

decreased with increasing delay intervals for the larger reward, providing empirical evidence of delay discounting: the value of money systematically declines as the money becomes more distant (Odum, 2011a; Rachlin et al., 1991; Rung et al., 2018).

In the **titrating alternatives task** participants also select between smaller-sooner and larger-later hypothetical monetary alternatives. Nonetheless, instead of presenting a fixed list, the immediate reward amount is manipulated based on the subject's previous choice, while the delayed amount remains constant. Du and colleagues (2002) instructed participants to make six choices for each of seven delays (1 month, 3 months, 9 months, 2 years, 5 years, 10 years, and 20 years). For example, they chose between obtaining \$100 now or \$200 in three months. Then, the immediate amount for the next five choices was adjusted depending on the previous choice. The amount of the next immediate reward was decreased when the subject selected the immediate reward, and increased if they chose the delayed reward. The size of this adjustment decreased by 50% with each subsequent choice. Continuing with the example above, if the participant chose the \$100 over \$200 in three months initially, the subsequent choice was between \$50 immediately and \$200 in three months. If they again selected the immediate \$50, the next choice would be between receiving \$25 now and \$200 in three months, and so forth. This procedure continued over six choices at each delay, narrowing the range of subjective values on subsequent choices until reaching the indifference point (Du et al., 2002). Hypothetical monetary rewards offer the advantage of practicality by enabling researchers to use a wide range of reward amounts and delays that hold significance for participants (Frederick et al., 2002). However, the validity of findings derived from choices about hypothetical monetary rewards has been questioned by researchers (e.g. Bickel & Marsch, 2001). Participants may lack the motivation to engage fully in the task or the ability to respond accurately as if they would genuinely receive the money (Frederick et al., 2002). To address these potential shortcomings, some studies favor an experiential task design using real monetary rewards, allowing participants to

actually experience delays and outcomes (e.g. Lagorio & Madden, 2005; Seinstra et al., 2018). Nevertheless, there is yet no evidence indicating that the nature of the reward (whether hypothetical or real) employed in delay discounting tasks affects participants' choices (Lagorio & Madden, 2005). Therefore, the evidence supports the notion that hypothetical rewards serve as valid representatives for real choices and are practical for studying delay discounting (Lagorio & Madden, 2005; Matta et al., 2012; Sellitto et al., 2010). However, humans do not exclusively discount monetary rewards. Over the past decades, researchers have investigated a variety of non-monetary outcomes such as food (e.g. DeHart et al., 2018), health (e.g. Chapman, 1996), entertainment (e.g. Charlton & Fantino, 2008), alcohol (e.g. Yankelevitz et al., 2012), or cigarettes (e.g. Yi & Landes, 2012), some of which will be referred to later in this thesis (see Odum et al., 2020 for a comprehensive review of non-monetary rewards).

3.2.3 The influence of trait and state effects on Delay Discounting

Delay discounting, the process of devaluing future rewards, is affected by both trait and state influences (Odum, 2011b). **State effects on delay discounting** refer to transient changes in an individual's discounting behavior (i.e. the steepness of discounting) due to contextual variables occurring within a short time frame. These variables include the type and the magnitude of rewards, as well as the context of the decision (Odum, 2011b; Odum et al., 2020). Regarding the type of reward, studies have consistently shown state effects on delay discounting, particularly the tendency for steeper discounting of non-monetary delayed rewards relative to monetary rewards (e.g. Bickel et al., 1999; Chapman, 1996; Estle et al., 2007; Madden et al., 1997; Odum, 2011a; Odum & Rainaud, 2003; Petry, 2001, 2003). Additionally, research such as that conducted by Green and colleagues (1997) has revealed that as the magnitude of the delayed reward increases, delay discounting becomes less steep (i.e. 'magnitude effect'). Lastly, the context in which the choice is made can also influence the degree of delay

discounting (Odum, 2011b; Odum et al., 2020). For instance, consumers' discount rates vary across different product contexts such as health, finance, and vacation (Foxall et al., 2011). Similarly, the context of gambling can impact the degree of delay discounting observed in pathological gamblers, depending on whether they are in their natural gambling context (e.g. a betting facility) or not (Dixon et al., 2006). Yet, delay discounting is influenced not only by state effects, but also by trait effects (Odum, 2011b; Odum et al., 2020).

Traits are commonly defined as “relatively enduring patterns of thoughts, feelings, and behaviors that reflect the tendency to respond in certain ways under certain circumstances” (Roberts, 2009, p.4). Therefore, **trait influences on delay discounting** represent pre-existing and relatively stable characteristics of individuals, impacting the extent to which they devalue future outcomes. Evidence supporting trait effects on delay discounting encompasses various forms, including the study of its reliability. By investigating test-retest reliability, cross-context reliability, and cross-outcome reliability, researchers can demonstrate the consistent response pattern of delay discounting, fulfilling one of the key requirements for defining it as a trait. This implies that delay discounting remains consistent over time (i.e. test-retest reliability), across different contexts (i.e. cross-context reliability), and regarding various outcomes (i.e. cross-outcome reliability). **Test-retest reliability** is typically evaluated by administering the same task version on two separate occasions, requiring participants to return to the testing environment for retaking the test (i.e. same-form reliability, Odum, 2011b; Odum et al., 2020). Research suggests robust test-retest reliability, with studies indicating strong consistency over test-retest intervals ranging from one week (e.g. Matusiewicz et al., 2013) to up to two years (e.g. Anokhin et al., 2015). As noted before, the study of Dixon and colleagues (2006) provides evidence of state effects on delay discounting, revealing higher discount rates among pathological gamblers in gambling compared to non-gambling contexts. Although this finding suggests context-dependency in delay discounting, their data also unveiled a strong positive correlation

between the degree of delay discounting in the two contexts, indicating that individuals who steeply discount rewards in one context do so in other contexts as well (a trait effect) (Dixon et al., 2006; Odum et al., 2020). A prevalent approach to determine trait effects on delay discounting through reliability studies involves exploring **cross-outcome reliability**. Studies in this domain usually investigate the correlation between an individual's discounting of one outcome and their discounting of another outcome (Odum, 2011b; Odum et al., 2020). It has been noted previously that individuals tend to discount different types of rewards to a different degree (e.g. Petry, 2001), which reflects a state effect (Odum, 2011b; Odum et al., 2020). However, if variations in discount rates are attributed to trait influences, one would expect consistent steep discounting regardless of the reward type, indicating a direct relationship between discount rates across outcomes (Green & Myerson, 2010). Several studies have identified such associations, reporting strong positive correlations between discount rates for monetary and those for non-monetary outcomes such as food (e.g. Demurie et al., 2013; Odum & Rainaud, 2003), entertainment (Charlton & Fantino, 2008), marijuana (M. W. Johnson et al., 2010), and alcohol (e.g. Friedel et al., 2014; Yankelevitz et al., 2012) (refer to Odum et al., 2020 for a comprehensive review of correlations between monetary and non-monetary rewards). Furthermore, personality variables operate as trait influences being related to variations in individuals' preferences for rewards over time (Manning et al., 2014). For instance, studies have revealed greater discount rates among individuals scoring higher on extraversion (Hirsh et al., 2008; Ostaszewski, 1996), those with a heightened sense of powerlessness regarding the future (indicated by scores on the Present-Fatalistic subscale of the Stanford Time Perception Inventory, M. W. Johnson et al., 2010), with a higher agreeableness (Miller et al., 2008), and those scoring lower on openness (Mahalingam et al., 2014). Additionally, higher neuroticism is associated with a greater preference for immediate rewards, while higher conscientiousness predicts lower discount rates (Mahalingam et al., 2014; Manning et al., 2014). Both, neuroticism and

conscientiousness are linked to impulsivity (Carver, 2005). Given that impulsivity is integral to human behavior and can also be measured as a trait, it is inherently linked to delay discounting (Carver, 2005; Manning et al., 2014). Thus, individuals' discounting behavior is thought to reflect their impulsivity level, with greater impulsivity being associated with increased discount rates and difficulty resisting immediate rewards, emphasizing its significance in delay discounting research (Diekhof et al., 2012; Sripada et al., 2011).

3.2.4 Impulsivity

Impulsivity is commonly recognized as a multidimensional construct that encompasses several facets contributing to decision-making processes. Among these facets, some authors propose that it includes motor impulsivity, often referred to as impulsive action. This aspect is thought to reflect a diminished capacity for inhibitory control over outward behavior. A further facet is the impulsive personality trait, indicating an individual's ability to self-regulate dominant preferences (MacKillop et al., 2016; Steward et al., 2017), which can be assessed through self-report measures such as the Barratt Impulsiveness Scale (Patton et al., 1995). Lastly, **impulsive choice** is characterized as an individual's decision-making style (MacKillop et al., 2016; Steward et al., 2017). According to Ainslie (1975), impulsive choices occur when individuals willingly opt for the immediate but inferior reward among two alternatives, even when fully aware of the options. Consequently, impulsivity is linked to the tendency to discount delayed rewards, making delay discounting in intertemporal choices a recognized measure of impulsivity today (Ainslie, 1975; Matta et al., 2012). Individuals who tend to discount rewards more steeply, show a preference for immediate rewards, even if they are of lesser value. Thus, since waiting would lead to a larger reward, these choices are often regarded as impulsive (Herman et al., 2018; Moreira & Barbosa, 2019). In this context, the inability to wait is thought to

reflect a lack of self-control⁶, which is crucial for favoring and maintaining commitments to important long-term goals (Ashe & Wilson, 2020; Shamosh & Gray, 2008). Such a deficit can lead individuals to make suboptimal intertemporal choices (i.e. steep delay discounting), thereby contributing to maladaptive behaviors including addictions (e.g. DeHart et al., 2018). Addictions in turn, are characterized by increased discount rates and individuals hypothesized to display greater impulsivity (Bickel et al., 1999; Herman et al., 2018a; Jentsch et al., 2014). In line with this perspective, individuals abusing a wide range of substances ranging from nicotine to cocaine and heroin, consistently show steeper discounting of delayed rewards compared to controls (Bickel et al., 1999; Kirby & Petry, 2004; Madden et al., 1997; Reynolds et al., 2004). Despite its multidimensional nature, many researchers describe impulsivity as a singular personality trait that impacts delay discounting (Manning et al., 2014; Sripada et al., 2011). Yet, within this context, some questions arise: Does impulsivity truly represent a unitary trait consistently influencing delay discounting across various commodities? And what precisely is the nature of the relationship between delay discounting and impulsivity?

Some authors (e.g. Green & Myerson, 2010; Takahashi et al., 2007) propose that understanding impulsivity in the realm of delay discounting requires distinguishing between two psychological processes. On one hand, individuals may exhibit an aversion to the uncertainty associated with delayed rewards, leading to greater discounting, and respectively, making an impulsive intertemporal choice. In this case, a greater discount rate should be interpreted not as a deficit in self-control, but rather a forward-looking and precautionous inclination (i.e. precautionous uncertainty aversion). On the other hand, impulsive intertemporal choices can arise from an aversion to waiting for delayed rewards, referred to as impatience or ‘pure time preference’. Individuals who are described as being unable to wait may thus have a deficit in self-control

⁶ Self-control, “the capacity to decouple behavior from a strongly desired, but suboptimal reward option” (Diekhof et al., 2012, p. 2), is usually operationalized as the opposite of making impulsive choices (Rachlin & Green, 1972)

(Takahashi et al., 2007). Evidence supporting these two underlying processes – precautionary uncertainty aversion and impatience (or pure time preference) – of impulsivity in delay discounting emerges from research involving gamblers (Moreira & Barbosa, 2019). Gambling behavior typically includes taking risks through a series of impulsive choices, despite uncertain outcomes and potential long-term negative effects (Holt et al., 2003). Consequently, gamblers tend to opt for the smaller, uncertain immediate options, entailing the possibility of winning money, over larger, more certain delayed rewards associated with saving money (Petry & Casarella, 1999). If impulsivity is a common underlying trait, one would expect a negative correlation between discounting of probabilistic and temporal rewards. This reflects the idea that individuals with addictions (i.e. impulsive) such as gamblers, exhibit both risk-taking behavior and an inability to delay gratification, manifesting as an increased preference for uncertain rewards and a decreased preference for delayed rewards (Green & Myerson, 2013; Luhmann, 2009). Contrary to this predicted negative correlation posited by a unitary impulsivity trait, substantial evidence suggests that a single common impulsivity trait does not fully explain these discounting patterns. To investigate this idea of ‘multiple impulsivities’ within the context of delay discounting, researchers frequently conduct correlational studies to assess the relationship between the discounting of delayed and probabilistic rewards. (Green & Myerson, 2013).

For example, Holt and colleagues (2003) investigated the association between different behavioral assessments of delay discounting and impulsivity. They aimed to determine whether performance on tasks measuring temporal and probabilistic discounting reflects a shared underlying trait of impulsivity. If impulsivity were a common factor, one would expect a negative correlation between scores on temporal and probabilistic discounting tasks. Specifically, individuals with high impulsivity levels, such as gamblers, would exhibit steep temporal discounting, indicating less concern for the long-term consequences of their choices. At the same time, one would expect them to show shallower probabilistic discounting due to reduced sensitivity

to uncertainty. To test this hypothesis, the authors instructed both gambling and non-gambling participants to perform tasks involving temporal and probabilistic discounting, aiming to evaluate potential differences in the degree of discounting between the two groups. In both types of tasks, participants chose between two hypothetical amounts of money. For temporal discounting, the authors implemented a typical amount-adjustment procedure (i.e. titrating alternatives task) involving two delayed amount conditions (\$1000 versus \$50,000) across seven delays (2 weeks, 1 month, 6 months, 1 year, 3 years, 5 years, and 10 years). Similarly, in the probability discounting task, they used an analogous amount-adjustment procedure and the same delayed amount conditions, with participants being studied across seven probabilities of receiving the reward (95, 90, 75, 55, 30, 10, and 5%). However, correlational analyses conducted within each group did not reveal the expected negative association between temporal and probabilistic discounting, which would have indicated a general impulsivity trait. Despite gamblers displaying shallower discounting of probabilistic rewards, indicating a higher inclination toward risk-taking, they did not show steeper discounting for delayed rewards (Holt et al., 2003). Another approach for exploring the relationship between probabilistic and temporal discounting took into consideration smokers, who are also characterized as impulsive (Green & Myerson, 2013). While smokers are known to exhibit higher degrees of discounting of delayed rewards (e.g. Bickel et al., 1999; Snider et al., 2020; Yi & Landes, 2012), based on the hypothesis that impulsive individuals are less influenced by the odds against winning, one might predict them to show shallower discounting of probabilistic rewards (Green & Myerson, 2013). However, numerous studies investigating the discounting behavior of smokers have provided substantial evidence indicating steeper (not shallower) discounting of probabilistic rewards compared to non-smokers (e.g. Reynolds et al., 2004; Yi et al., 2007).

In summary, the steepness of individuals' discounting is thought to mirror their level of impulsivity. From this perspective, impulsivity manifests as a consistent underlying trait

influencing the degree to which people discount delayed and probabilistic rewards (Green & Myerson, 2010, 2013). However, results from correlational studies contradict this conceptualization of impulsivity, which links impatience with risk-taking (Green & Myerson, 2010). Instead they underscore the idea of dissociating impulsivity in delay discounting into two distinct sub-processes (Takahashi et al., 2007). Overall, a nuanced understanding of impulsivity within the context of delay discounting is critical for developing effective medical interventions and challenges the notion of a general trait hypothesis of impulsivity, which suggests that impulsive individuals, whose decisions are affected by the delay until the receipt of a reward are simultaneously less influenced by the uncertainty surrounding reward delivery (Green & Myerson, 2013; Holt et al., 2003; Takahashi et al., 2007). However, solely focusing on problematic behavior by comparing extreme groups (e.g. substance abusers versus controls) to understand the relationship between impulsivity and delay discounting may not be representative of behavioral tendencies in the broader population (Green & Myerson, 2010). Further research is necessary to explore whether the association between delay discount rates and impulsivity holds true in healthy populations as well (Moreira & Barbosa, 2019).

3.2.5 Neural bases of Delay Discounting

While delay discounting is widely studied through behavioral approaches, researchers are also interested in the neural correlates underlying intertemporal decision-making (e.g. Ballard & Knutson, 2009; Kable & Glimcher, 2007, 2010; McClure et al., 2004, 2007). Remarkably, evolutionary parallels in the phenomenology of delay discounting are observed across species (Rosati et al., 2007; Vanderveldt et al., 2016), indicating a promising starting point for translational research employing animal models to understand the neural mechanisms of delay discounting in humans (Moro et al., 2023). Animal studies have linked orbitofrontal cortex (OFC) activity to intertemporal choices (Sosa et al., 2021), as demonstrated in studies

with monkeys (e.g. Hosokawa et al., 2013) and rats (e.g. Roesch et al., 2006). Lesions to the OFC in these animals result in alterations in delay discounting, with some studies reporting increased discount rates (Mobini et al., 2002; Rudebeck et al., 2006) and others revealing a shift of the animals' preference towards the delayed reward (i.e. decreased discount rates) (Mar et al., 2011; Winstanley et al., 2004). Although findings from animal studies demonstrate contrasting outcomes, in humans, lesions to the OFC – particularly the medial OFC (mOFC) – lead to a significant increase in individuals' preference for the smaller, immediate reward over the larger, delayed one. Consequently, individuals with such lesions show steeper delay discounting (Sellitto et al., 2010). In general, neuroimaging studies have identified a key set of brain regions engaged when making choices between rewards available at different time points, including the medial prefrontal cortex (mPFC), the posterior cingulate cortex (PCC), and the ventral striatum (VS) (Kable & Glimcher, 2007, 2010; McClure et al., 2004, 2007). Researchers have used various approaches aiming to clarify the functions of these neural substrates of intertemporal decision-making (Peters & Büchel, 2011; Sripada et al., 2011).

One conceptual framework is the **'two-system model'**, which posits that mPFC, PCC, and VS are particularly sensitive to the availability – thus the presence or absence of an immediate reward (McClure et al., 2004, 2007). Inspired by Laibson's (1997) β - δ model, the authors hypothesized the engagement of two distinct neural systems when making intertemporal choices (McClure et al., 2004, 2007). The impulsive (β) system, exclusively reflects the value of immediate rewards and is responsible for impatient choices, whereas the more patient and rational (δ) system consistently values both immediate and delayed rewards (Laibson, 1997). Consistent with this hypothesis, McClure and colleagues (2004, 2007) found differential engagement of these systems when individuals make intertemporal choices, with each system being associated with distinct brain activation patterns (McClure et al., 2004, 2007). Specifically, the mPFC, PCC, and VS are implicated as forming the basis of the β -system, showing

significantly higher activation during intertemporal choices involving immediate rewards compared to those involving delayed rewards. In contrast, the lateral prefrontal cortex and the posterior parietal cortex were consistently activated across all types of choices, irrespective of reward delay, indicating their association with the δ -system (**Fig. 3**; McClure et al., 2004, 2007). More important, while initially using only monetary rewards (McClure et al., 2004), findings from this study were replicated and extended in a subsequent experiment using primary rewards such as juice and water. Those results reaffirmed that the β -system showed greater activation when immediate options were present, while the δ -system remained insensitive to reward immediacy, showing consistent activation regardless of the temporal characteristics of the available rewards (McClure et al., 2007).

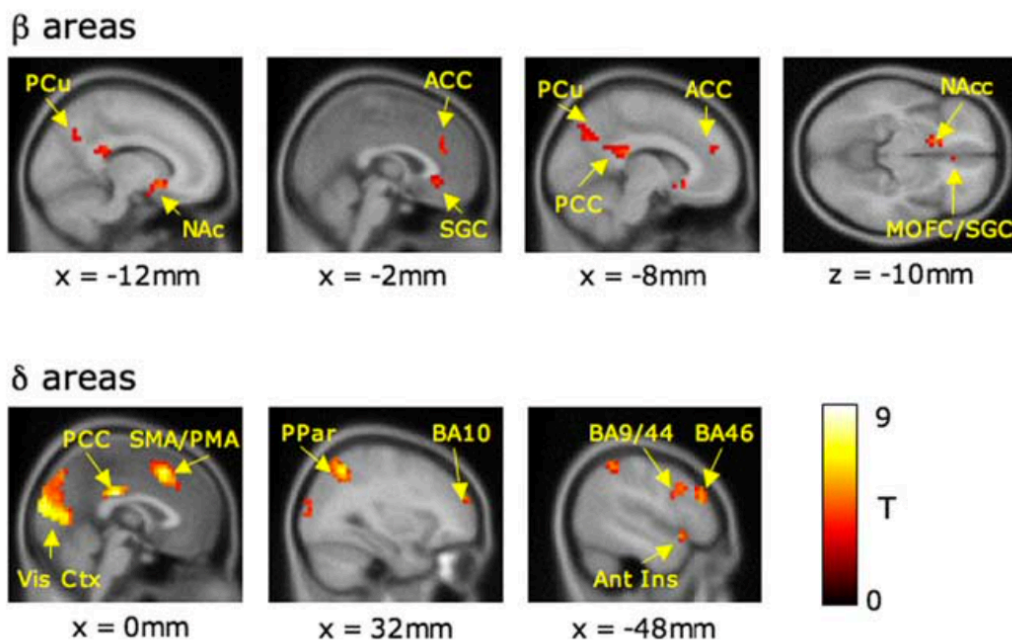


Figure 3. fMRI data supporting the two-system model of intertemporal choice. The upper panel depicts regions associated with the impulsive system (β areas), which show heightened activation during intertemporal choices featuring immediate rewards. The bottom panel displays regions linked to the patient and rational system (δ areas), which are activated across all intertemporal choices regardless of immediacy (Adapted from McClure et al., 2007).

Nevertheless, the hypothesis that mPFC, PCC, and VS are exclusively activated in response to the availability of immediate rewards, as proposed by McClure and colleagues (2004, 2007), was scrutinized and ultimately falsified by Kable and Glimcher (2007, 2010). They proposed a link between the subjective value individuals assign to available rewards and the activation observed in mPFC, PCC, and VS during intertemporal decision-making. In their study (Kable & Glimcher, 2007), they employed a psychometric-neurometric approach⁷ to determine whether neural activity in these brain regions tracks the subjective value of delayed monetary rewards. Participants were presented with a choice between a fixed reward, immediately available, and a delayed reward of varying magnitudes, while neural activity was measured using functional magnetic resonance imaging (fMRI). The results revealed a correlation between activation in the mPFC, PCC, and the VS and the participants' individual preference curves, reflecting alterations in subjective values as a function of delay and amount (**Fig. 4a**; Kable & Glimcher, 2007). This correlation was evident during the presentation of delayed rewards (approximately 6-10 s into the trial). Moreover, as hypothesized by the researchers, these areas showed increased activity with an increase in the objective amount of the delayed reward, diminished activity with prolonged delay to receipt, and enhanced activation when participants opted for the delayed reward due to its perceived higher value (**Fig. 4b-e**; Kable & Glimcher, 2007). Consequently, they contested the notion of the exclusive specificity of these regions for immediate rewards (McClure et al., 2004, 2007), suggesting instead that mPFC, PCC, and VS encode the subjective value of delayed rewards (Kable & Glimcher, 2007), now collectively known as **'single system model'**.

⁷ Psychometric-neurometric methods test “whether a particular, externally quantifiable variable influences both psychophysical and neurobiological measurements in a similar manner” (Kable & Glimcher, 2007).

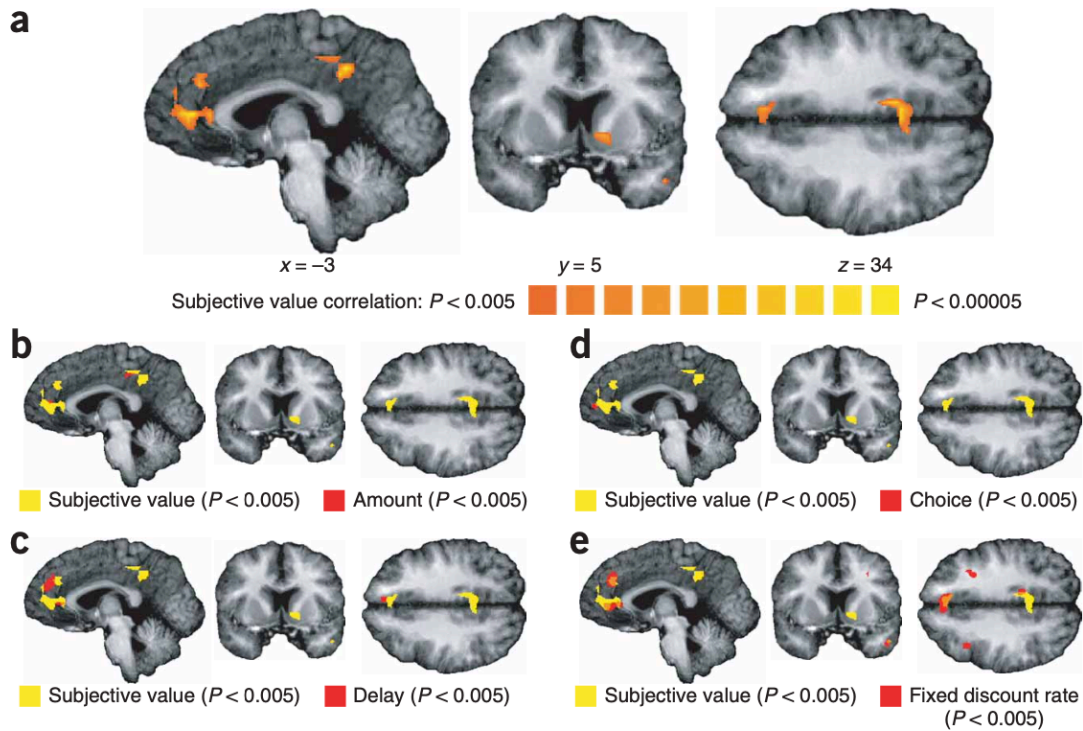


Figure 4. Brain regions whose activation correlates with individuals' subjective values during the presentation of delayed rewards. Panel (a) presents anatomical images of the brain with highlighted areas where such correlations are observed, including the mPFC on the left, the PCC on the right, and the VS in the middle image. Panels (b-e) demonstrate that activity in the mPFC, the PCC, and the VS is better explained by subjective value rather than objective aspects of the delayed reward, such as the monetary amount (b), the delay of the reward (c), the choice of the participant (delayed > immediate reward) (d), and the value of the delayed reward computed using a single fixed discount rate for all participants (e). Activity in brain areas correlated with subjective values are presented in yellow, while correlations with the other variables are shown in red, with overlaps depicted in orange (Adapted from Kable & Glimcher, 2007).

However, unlike McClure and colleagues (2004, 2007), Kable and Glimcher (2007) did not include an experimental condition in which both rewards were delayed. To address this limitation, they conducted another experiment (Kable & Glimcher, 2010), reporting behavioral and fMRI results. Contrary to implications of studies relying on hyperbolic models, they did not observe the typically preference reversals expected, where individuals shift from favoring the smaller, immediate reward to choosing the larger, delayed reward when both options are postponed. Subjects indeed exhibited decreasing impatience when making choices between two delayed rewards. However, this decrease in impatience was influenced by the delay between

the two rewards, meaning that participants assigned greater values to the soonest possible rewards, regardless of whether they were available immediately or later in time. Additionally, the activation observed in the mPFC, PCC, and VS correlated with both immediate and delayed rewards, suggesting that these regions encode subjective values on an absolute scale, which also depends on the temporal distance from the present (**Fig. 5**; Kable & Glimcher, 2010). To reconcile these findings, Kable and Glimcher (2010) introduced the ‘**As Soon As Possible (ASAP) model**’ as alternative to the commonly used hyperbolic discounting models. Unlike these models that assume subjective values decline relative to the present, the ASAP model proposes that subjective values decline hyperbolically, but relative to the soonest possible reward, irrespective of its immediacy (Kable & Glimcher, 2010). These results again challenge the conclusion drawn by McClure and colleagues (2004, 2007), suggesting that the greater activation exhibited by the mPFC, PCC, and VS in response to the availability of immediate rewards solely occurs because these regions primarily value immediate rewards. Instead, it suggests that immediate options may merely be subjectively more valuable compared to delayed ones (Kable & Glimcher, 2007, 2010).

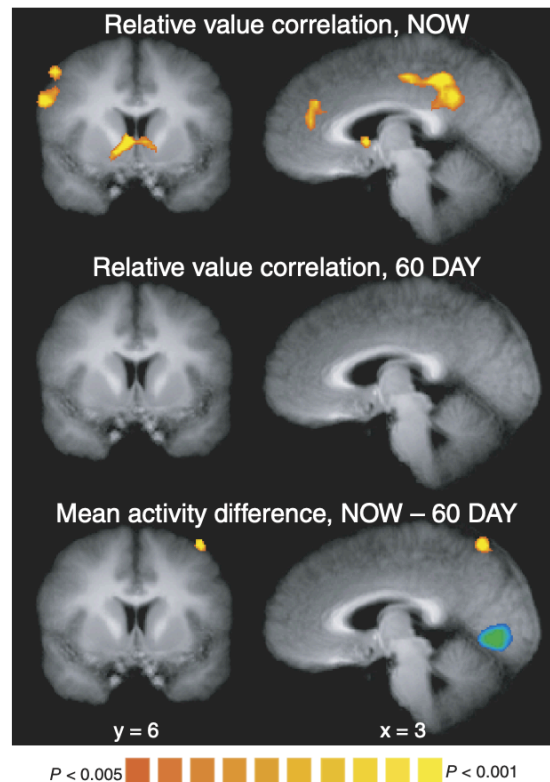


Figure 5. Three effects of interest are shown. The correlations between activation and subjective value in the NOW condition (top), the 60 DAY condition (middle), and the difference in mean activation between the two conditions (bottom) (Adapted from Kable & Glimcher, 2010).

Peters and Büchel (2011) proposed a third neural account, suggesting that the neural bases underlying intertemporal choice involve neural circuits supporting different aspects of intertemporal decision-making. This so-called ‘**self-control model**’ emphasizes that the VS and ventromedial OFC (also referred to as vmPFC or medial OFC) form a domain-general network that codes for subjective value irrespective of reward delay. In contrast, delay-specific signals emerge from the mPFC, PCC, and lateral parietal cortex. However, efficient choice behavior necessitates a common neural coding of stimulus value, and the authors propose that the core valuation network – comprising the VS and OFC – integrates the domain-specific information from the mPFC, PCC, and lateral parietal cortex into a unified neural currency (Peters & Büchel, 2009, 2010). Consequently, the vmPFC, VS, and PCC represent the subjective discounted value of all rewards, supporting the single valuation account of a unitary system, which

represents the value of both immediate and delayed rewards (Kable & Glimcher, 2007, 2010; Peters & Büchel, 2009, 2010b). Importantly, Peters and Büchel (2011) emphasize that efficient decision-making also requires self-control, highlighting the significant role of the PFC within a cognitive control network. Previous studies have indicated that the lateral PFC may be associated with the deployment of self-control during decision-making (Hare et al., 2009). Accordingly, they suggest that the valuation system is subject to top-down control by the lateral PFC, which modulates the value signals in the vmPFC.

While previous research has presented conflicting perspectives, either focusing on a two-component (McClure et al., 2004, 2007) or on a one-component model of delay discounting (Kable & Glimcher, 2007, 2010; Peters & Büchel, 2009, 2010b), an additional approach emphasized by Ballard and Knutson (2009) offers further insight. This account not only provides evidence for activation in limbic and lateral brain regions but also sheds light on the potential dissociation of the neural substrates associated with the magnitude and delay of future rewards. In their study, Ballard and Knutson (2009) employed a parametric delay discounting task coupled with event-related fMRI. This task was structured in a temporal sequence, where participants were presented with staggered information. Initially, they were shown a fixed immediate reward (\$10.00 at a delay of 0 days). Subsequent screens displayed the magnitude and then the delay of the future reward. Finally, participants were prompted to choose between the immediate and delayed options (**Fig. 6**; Ballard & Knutson, 2009).

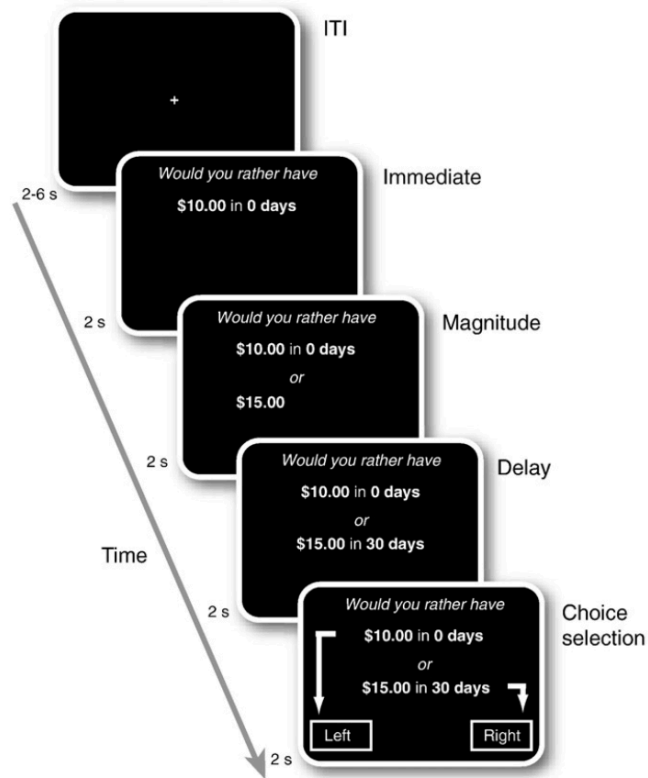


Figure 6. Example trial from the task, characterized by staggered presentation of information regarding the magnitude and delay of future rewards. Initially, the first screen (2 s) displayed the immediate reward with a fixed amount and delay (\$10 at a delay of 0 days). Subsequently, the second screen (2 s) presented the magnitude of the delayed reward, which varied across seven amounts in total (\$10.00, \$10.50, \$11.00, \$15.00, \$20.00, and \$25.00). The following screen (2 s) indicated the delay of the future reward, varying across six delays (0, 7, 30, 60, 90, and 180 days). Finally, participants were prompted to make a choice between the two options on the fourth and last screen (2 s). Each trial concluded with a variable inter-trial interval (ITI) lasting 2 to 6 s (Adapted from Ballard & Knutson, 2009).

This procedure allowed researchers to isolate brain activity associated with reward magnitude and delay. The neuroimaging results revealed a positive correlation between activation in the nucleus accumbens (NAcc), the mPFC, and the PCC and increasing magnitudes of future rewards. Furthermore, activation in the dorsolateral prefrontal cortex (DLPFC), the temporo-parietal junction (TPJ), and the posterior parietal cortex negatively correlated with increasing delays of future rewards (Ballard & Knutson, 2009). Additionally, Ballard and Knutson (2009) investigated potential correlations between the neural activity in these regions in response to

reward magnitude and delay and each participant's discount rates. These analyses revealed a negative correlation between individual differences in neural responsiveness to reward magnitude and discount rates, particularly in the NAcc. Moreover, individual differences in deactivation of the DLPFC and the posterior parietal cortex correlated with discount rates. Therefore, more impulsive individuals exhibited lower activation in response to larger reward magnitudes, while displaying greater deactivation for longer delays until receiving a reward (Ballard & Knutson, 2009). Overall, these findings offer some alignment with both the two-component model (McClure et al., 2004, 2007) and the one-component model (Kable & Glimcher, 2007, 2010). On one hand, the observed double dissociation of regions sensitive to magnitude (i.e. NAcc) and delay (i.e. DLPFC, TPJ, and posterior parietal cortex) of future rewards is consistent with McClure and colleagues' (2004, 2007) findings, suggesting that choosing a larger delayed reward recruits lateral cortical regions. However, the discovery of delay-related activation in regions previously associated with responding to reward magnitude (i.e. mPFC and PCC) leans towards the hypothesis of a single neural system being sensitive to both magnitude and delay (Kable & Glimcher, 2007).

More recently, Frost and McNaughton (2017) presented additional evidence for a multiple system perspective on delay discounting, emphasizing that it arises from interactions within several neural systems broadly distributed across the brain. Their review synthesized findings regarding brain regions involved in delay discounting from diverse studies focusing on different behavioral variables. These studies examined aspects such as subjective value, delay of rewards, availability of an immediate reward, and discount measures like k and AUC (refer to Frost & McNaughton, 2017 for a comprehensive review). Unlike previous studies, Frost and McNaughton (2017) identified activity related to delay discounting across a range of brain regions including the thalamus, sensory, parietal, temporal, cingulate, prefrontal, motor, and insular cortex, and basal ganglia. Drawing from their findings, they constructed a basic

neural model encompassing both the cognitive and neuroanatomical aspects of the neural systems implicated in delay discounting. At the cognitive level, Frost and McNaughton (2017) propose a five-stage processing framework whereby signals from delay discounting tasks are converted into neural signals and processed by the relevant neural systems. These stages involve: system 1, responsible for sensory stimulus perception; system 2, which extracts reward-related information from sensory input; system 3, entailing representations of immediate and delayed reward values; system 4, serving as a comparator system for selecting between alternative options; and finally, system 5, comprising two sub-systems – one responsible for motor response generation and the other for response inhibition. Their schematic representation, depicted in **Figure 7**, presents the areas activated during delay discounting and illustrates the flow of information in the brain (see Fig. 3 in Frost & McNaughton, 2017 for a detailed schematic representation). Importantly, information does not merely occur in a linear fashion but can circulate in recurrent loops (Frost & McNaughton, 2017).

Each of the studies mentioned (Ballard & Knutson, 2009; Frost & McNaughton, 2017; Kable & Glimcher, 2007, 2010; McClure et al., 2004, 2007; Peters & Büchel, 2009, 2010b, 2011) exhibits notable differences in their analyses, hindering a straightforward comparison of their findings. Consequently, further research is warranted to reconcile these discrepancies. However, despite their schematic summaries maintaining an atheoretical stance, Frost and McNaughton (2017) offer a neural model that could serve as a foundational framework for integrating the diverse findings in this field. Additionally, it provides a platform for further research of the individual components of the model itself and the precise role of the neural substrates involved in delay discounting, which remain incompletely understood to date (Frost & McNaughton, 2017).

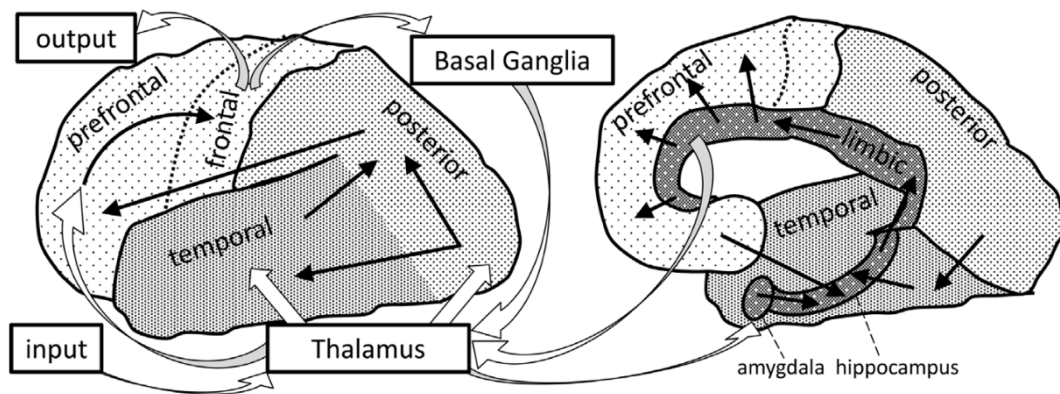


Figure 7. Connectivity of the major brain areas involved in delay discounting, presented in a 3D representation of the brain. Initially, sensory information (system 1) reaches the thalamus before being transmitted to the posterior cortex for visual input and the temporal cortex for auditory input. From here, the information is directed to the junction between the temporal and posterior cortex, where it proceeds to the PFC, and eventually to the motor cortex in the frontal cortex to generate output. Beyond its role as primary sensory relay, the thalamus also plays a crucial part in feedback loops, such as those controlling the selection and timing of outputs via the basal ganglia to the cortex (frontal cortex – basal ganglia – thalamus – prefrontal cortex – frontal cortex). Additionally, there exists a feedback loop between the cortex and hippocampus, which includes the amygdala, hippocampus, and limbic cortex, responsible for adjustments related to motivation and memory (Adapted from Frost & McNaughton, 2017).

Human decision-making is invariably characterized by the need to weigh consequences of choices spread across time, known as intertemporal choices (Ericson & Laibson, 2019; Matta et al., 2012). Central to understanding these decisions is the phenomenon of delay discounting, which sheds light on how individuals navigate options with varying temporal outcomes (e.g. Sellitto et al., 2011). Through diverse experimental approaches, researchers consistently observe a preference for smaller immediate rewards over larger delayed ones, particularly in clinical populations believed to exhibit heightened impulsivity (Ainslie, 1975; Diekhof et al., 2012; Sripada et al., 2011). Consequently, studying delay discounting offers crucial insights into fundamental aspects of human behavior and decision-making processes, with direct clinical relevance for conditions such as addiction, obesity, and substance abuse (e.g. Dixon et al., 2003; Sellitto et al., 2011). Investigating mechanisms that modulate delay discounting in these populations is essential for promoting long-term health outcomes (e.g. Frederick et al., 2002).

Research indicates that deficits in interoception (e.g. Martin et al., 2019; Robinson et al., 2021) and various memory processes (e.g. Bromberg et al., 2017; Lempert et al., 2017) contribute to individuals' propensity for immediate gratification, leading to adverse health consequences over time. The following chapters of this thesis delve into interoception and memory as potential influencers of delay discounting, examining relevant research findings within the context of intertemporal choice (among clinical populations). Moreover, they aim to explore the potential interconnections between these three factors, offering a comprehensive understanding of their roles in intertemporal decision-making processes.

4 Methods

The search for original and review research articles was conducted in April 2024, utilizing the databases Web of Science, PubMed, and Google Scholar. The search terms and categories used are listed in **Table 1**. Within each category, terms were combined using the Boolean operator ‘OR’, while the categories themselves were combined using the Boolean operator ‘AND’.

Table 1

Search terms and categories used for literature research

Delay discounting	Interoception	Memory
delay discounting	interocept*	autobiographical memory
intertemporal choice		mental time travel
temporal discounting		episodic future thinking

This approach resulted in two distinct search strings: (1) for the relationship between **delay discounting and interoception** (((("delay discounting") OR ("intertemporal choice") OR ("temporal discounting")) AND (interocept*)), and (2) for the relationship between **delay discounting and memory** (((("delay discounting") OR ("intertemporal choice") OR ("temporal discounting")) AND (("autobiographical memory") OR ("mental time travel") OR ("episodic future thinking"))). The search was restricted to articles written in English and involving human participants. The first search string resulted in 15 articles on PubMed, 19 on Web of Science, and 5,540 on Google Scholar totaling 5,521 articles on the relationship between delay discounting and interoception. The second search string revealed 681 articles on Pub Med, 175 on Web of Science, and 3,780 on Google Scholar. Titles and abstracts of the identified and non-overlapping articles were screened for relevance, and the full texts of potentially relevant articles were assessed for eligibility based on if they elaborate on the relationship between the mentioned concepts and/or investigate clinical populations such as obesity and addictions.

5 The impact of Interoception on Delay Discounting

Interoception is highly pertinent across various realms of human life, encompassing psychological and health-related domains, thereby warranting attention in both research and theory (Ceunen et al., 2016). Much like delay discounting, it holds a pivotal role in bodily and mental functions, significantly impacting individuals' overall health and well-being (Schmitt & Schoen, 2022). Notably, research has identified deficits in interoception as risk factors for dysfunctional decision-making, highlighting its potential relevance in delay discounting studies (Martin et al., 2019; Volkow & Baler, 2015). This chapter aims to outline the current consensus on the definition of interoception and its assessment, stressing the importance of exploring interoception within the context of delay discounting.

5.1 Unraveling the definition of Interoception: Toward an inclusive perspective

Despite its longstanding presence in scientific discourse, a precise consensus regarding the definition of interoception remains elusive (Ceunen et al., 2016). Sherrington's (1906) seminal work "The Integrative Action of the Nervous System" outlined early conceptions of interoception alongside, exteroception and proprioception, within the context of sensory signal processing by the nervous system. He described exteroception being associated with stimuli from the external environment, while proprioception pertains to signals from deep somatic tissue such as skeletal muscles. In contrast, interoception was characterized by signals originating internally within the viscera (Sherrington, 1906). However, this traditional and restrictive understanding of interoception has evolved into a more inclusive conceptualization in contemporary discourse (Ceunen et al., 2016; Schmitt & Schoen, 2022). Craig (2002) pioneered this shift by redefining interoception as the perception of the physiological status of the entire body, including all tissues rather than just the viscera. Building upon Craig's (2002) concept, modern scholars widely endorse the idea of interoception as subjective perception of bodily signals and

states, integral to constructing a representation of the sensory experience imbued with meaning. Recognized as multidimensional system, interoception is thought to be a product of the central nervous system (CNS) (Ceunen et al., 2016; Messina et al., 2022; Schmitt & Schoen, 2022). A recent consensus statement emerging from the first Interoception Summit in 2016, solidifies this perspective, defining interoception as “the process by which the nervous system senses, interprets, and integrates signals originating from within the body, providing a moment-by-moment mapping of the body’s internal landscape across conscious and unconscious levels” (Khalsa et al., 2018, p.1). This bidirectional communication between the brain and body is paramount for maintaining homeostatic functioning, adapting to internal and external changes, and ensuring survival (Khalsa et al., 2018; Schmitt & Schoen, 2022; Wang & Chang, 2024). Hence, interoceptive processing spans all major biological systems involved in maintaining homeostatic balance, encompassing cardiovascular (e.g. Oppenheimer & Cechetto, 2016), pulmonary (e.g. Schroyen et al., 2016), gastrointestinal (e.g. Büttiker et al., 2021), nociceptive (e.g. Simons et al., 2014), chemosensory (e.g. Koeppl et al., 2020), thermoregulatory (e.g. Fealey, 2013), genitourinary (e.g. Drake et al., 2010), osmotic (e.g. Stevenson et al., 2024), visceral (e.g. Jänig, 1996), immune (e.g. Harrison et al., 2009), and autonomic systems (e.g. Critchley & Harrison, 2013). Importantly, interoception is not a unitary sensory domain, as complex changes in the internal states of the body, such as food ingestion, require the integration of multiple interoceptive signals emerging from various biological systems (Schmitt & Schoen, 2022; Wang & Chang, 2024). But how exactly do these signals get processed within the interplay between body and brain? Interoceptive processing is thought to involve a reciprocal circuit comprising both bottom-up and top-down processes. Ascending pathways deliver interoceptive signals regarding internal body states to the CNS (bottom-up), while descending control from the CNS regulates these internal states (top-down) (Berntson & Khalsa, 2021; Desmedt, Luminet, Maurage, et al., 2023). More precisely, chemical, mechanical, and thermal signals detected by

receptors within the body are converted into electrical or hormonal signals. These signals are then processed in subcortical brain structures and projected to higher cortical regions, such as the hypothalamus, insula, anterior cingulate cortex (ACC), and somatosensory cortex, where the interoceptive information is further interpreted (e.g. Berntson & Khalsa, 2021). Despite these physiological pathways and neural circuits of interoception operating across conscious and unconscious levels (Berntson & Khalsa, 2021), humans typically are not consciously monitoring their physiological state (Schmitt & Schoen, 2022; Suksasilp & Garfinkel, 2022). This suggests that preconscious interoceptive processes likely play a significant role (Schmitt & Schoen, 2022; Suksasilp & Garfinkel, 2022), with the majority of interoceptive processes occurring outside of conscious awareness (Khalsa et al., 2018). At the conscious level, Garfinkel and colleagues (2015) propose a three-dimensional model that distinguishes between (1) interoceptive accuracy, (2) sensibility, and (3) awareness. Interoceptive accuracy refers to the objective capacity to detect internal bodily signals, while interoceptive sensibility relates to self-reported subjective interoceptive experiences and the inclination to focus on them. Finally, interoceptive awareness involves metacognitive insight into interoceptive ability, as indicated by the correspondence between objective and subjective measures. These dimensions form the basis for widely used assessment tools to measure interoception, which will be detailed in the subsequent section of this thesis (Desmedt, Luminet, Walentynowicz, et al., 2023; Garfinkel et al., 2015; Tsakiris & Critchley, 2016).

5.2 Interoception measurement techniques and assessment tools

While the assessment of interoception remains somewhat inconsistent, frequently used measures of interoception typically focus on the three dimensions outlined above (Garfinkel et al., 2015; Suksasilp & Garfinkel, 2022). Firstly, **interoceptive accuracy** (1), the most studied dimension, is evaluated through performance-based tasks where measures are derived from the

relationship between objectively measured physiological events and participants' self-reported sensations. The cardiac domain stands out as the most thoroughly investigated bodily axis in this regard (Desmedt, Luminet, Walentynowicz, et al., 2023; Suksasilp & Garfinkel, 2022). Cardiac tasks are generally categorized into three types: heartbeat tracking tasks, two alternative forced-choice tasks, and multi-interval tasks (Brener & Ring, 2016). **Heartbeat tracking tasks** involve participants reporting the number of heartbeats sensed within a specified timeframe (Schandry, 1981), tapping in synchrony with each heartbeat (e.g. Couto et al., 2014; Kleinman, 1970), or adjusting the rate of external stimuli to match their heartbeat (Carroll & Whellock, 1980; Gannon, 1980). In **two alternative forced-choice tasks**, participants determine whether external stimuli, like light flashes or tones, are synchronous or asynchronous with their heartbeat (Whitehead et al., 1977). Notably, these tasks require more than chance guessing for successful completion, which is the main limitation of heartbeat tracking tasks (e.g. Desmedt et al., 2018). However, since most participants struggle to discriminate the stimuli, Brener and colleagues (1993) developed a **multi-interval task** based on the method of constant stimuli (Clemens, 1984) to address this limitation. In this task, participants judge whether a series of ten tones presented across several intervals align with or diverge from their heartbeat (Brener et al., 1993). Secondly, **interoceptive sensibility** (2) can be quantified using self-report questionnaires (e.g. Multidimensional Assessment of Interoceptive Awareness [MAIA]; Mehling et al., 2012 or Interoceptive Accuracy Scale [IAS]; Murphy et al., 2020) or confidence measures, assessing participants' subjective beliefs regarding their interoceptive accuracy during specific tasks (Garfinkel et al., 2015). Correlating these confidence scores (i.e. interoceptive sensibility) with behavioral task performance (i.e. interoceptive accuracy) is instrumental in predicting individuals' accuracy on a trial-by-trial basis, providing a metacognitive index of their interoceptive ability (Garfinkel et al., 2015; Suksasilp & Garfinkel, 2022). Within this framework, the meta-*d*' approach, which models the correlation between the 'Area Under the Receiver

Operating Characteristic' (D. M. Green & Swets, 1966)⁸ and task performance, yields unconfounded metacognitive measures and is currently the most precise measure of **interoceptive awareness** (3) (Fleming, 2017).

5.3 Exploring the interplay of Interoception and Delay Discounting

A growing body of research suggests a connection between delay discounting and interoception, particularly at the neural level (Halcomb et al., 2022; Sellitto et al., 2016; Volkow & Baler, 2015; Zhang et al., 2023). The pivotal role of the insula in homeostatic representation of the body and its involvement in decision-making processes (Craig, 2002, 2009; Volkow & Baler, 2015) underscores its significance as a target for investigating the potential link of interoception and delay discounting. Indeed, neuroimaging and lesion studies have focused on the insula, some of which are referred to in this chapter. Within this context, researchers have primarily examined clinical conditions such as disordered eating behavior (Zhang et al., 2023) and substance abuse (Halcomb et al., 2022) to determine whether interoception amplifies or diminishes delay discounting. Additionally, behavioral-level connections between delay discounting and interoception have been indicated by studies investigating emotions (Kochanowska et al., 2023; Scarpazza et al., 2017; Weafer et al., 2013).

5.3.1 Role of the insular cortex

The insula is the central CNS hub to integrate interoceptive signals related to the body and may influence the evaluation of different options in intertemporal choice situations. One

⁸ The AUROC is a metric commonly used to evaluate the performance of binary classification models across various decision thresholds (Narkhede, 2021). In the context of interoception research, ROC (Receiver Operating Characteristic) analyses gauge the degree to which a binary response (such as participants' confidence ratings regarding their perceived response accuracy) aligns with a binary state variable (e.g. correct or incorrect judgment on a heartbeat detection task) across all feasible thresholds. The AUC (area under the curve) of the ROC graph provides a precise quantification of the degree to which confidence ratings accurately reflect actual performance (Garfinkel et al., 2015).

possibility is, that is has a role in generating urges that guide decision-making behavior based on one's physiological states (Craig, 2009; Naqvi & Bechara, 2010; Volkow & Baler, 2015). In the study of Sellitto and colleagues (2016), patients with lesions to the insula, patients with damage outside the insula, and healthy controls performed a delay discounting task choosing between smaller-sooner and larger-later monetary rewards. Patients with insular lesions exhibited significantly reduced delay discounting compared to controls. These findings are consistent with other lesion studies indicating that insular lesions result in an apparent greater willingness to wait for delayed rewards, potentially due to a reduction in the perceived appeal toward the immediate reward (Fu et al., 2022; Naqvi et al., 2007).

5.3.2 Interoception and reduced immediate reward preference: The role of enhanced insula activation

Contrary to findings indicating reduced delay discounting associated with insula damage, some fMRI studies have reported the opposite trend, with higher insula activation correlating with decreased delay discounting (Halcomb et al., 2022; Zhang et al., 2023). This intersection between delay discounting and interoception is evident in studies focusing on food and disordered eating behaviors. Interoception, crucial for maintaining balanced internal states, guides decision-making by motivating behaviors such as seeking food to address depleted nutritional internal states (Maniscalco & Rinaman, 2018; Martin et al., 2019). Martin and colleagues' systematic review (2019) highlighted a consistent relationship between dysfunctional interoception and eating disorders, including anorexia nervosa (AN), bulimia nervosa (BN), and binge eating disorder (BED), with individuals diagnosed with these disorders exhibiting lower interoceptive awareness compared to healthy controls (refer to Abbate-Daga et al., 2014 for AN; de Vries & Meule, 2016 for BN; and Vinai et al., 2015 for BED). Additionally, deficits in interoception have been linked to higher BMI and obesity (Robinson et al., 2021),

given that excessive food consumption is a hallmark feature of obesity (Schiff et al., 2016). Internal signals, like circulating appetite hormones, play a crucial role in regulating food intake. In obese individuals, deficits in interoception may lead to reduced sensitivity to satiety signals, affecting their decision-making regarding food (Martin et al., 2019). Therefore, impaired interoceptive ability contributes to maladaptive food-related decisions, highlighting the potential role of delay discounting in the context of disordered eating. These interoceptive deficits may shape individuals' delay discounting behavior, leading to a consistent preference for immediate gratification, such as food intake, over long-term health benefits like maintaining a healthy body weight. Indeed, evidence suggests that obese individuals are prone to impulsive food choices, as they tend to succumb to the temptation of immediate edible rewards compared to normal-weight controls (Schiff et al., 2016). Additionally, steeper discounting in obese individuals is associated with higher BMI (Schiff et al., 2016), suggesting that overeating, resulting from the repeated preference for immediate food gratification, significantly contributes to maintaining an obese body weight (Bénard et al., 2019). Bariatric surgery, such as laparoscopic sleeve gastrectomy, is currently recognized as the most effective intervention for weight reduction in obesity (Arterburn & Gupta, 2018), while also improving disordered eating patterns (Zhang et al., 2023). Building on this premise, Zhang and colleagues (2023) investigated the impact of laparoscopic sleeve gastrectomy on reward-based intertemporal decision-making and its neural correlates in individuals with obesity. Employing fMRI, obese participants performed a monetary delay discounting task before and one month post-surgery. The study examined alterations in brain activation and functional connectivity pre- and post-surgery, comparing them to normal weight controls (Zhang et al., 2023). Results unveiled a significant decrease in discount rates in obese individuals post-laparoscopic sleeve gastrectomy compared to pre-surgery levels. Brain activation analyses revealed diminished activation in the DLPFC and heightened activation in the insula. The DLPFC, pivotal in representing reward delay in intertemporal decision-

making (Ballard & Knutson, 2009), is associated with the executive control network recruited for choices between alternatives with extended delays requiring inhibition of prepotent responses (e.g. McClure et al., 2004). A prior study by Zhang and colleagues (2022) noted obese individuals exhibiting hyperactivation in the DLPFC and reduced connectivity within the executive control network during intertemporal choices, indicative of neural inefficiency associated with higher discount rates. Thus, decreased hyperactivation of the DLPFC post-laparoscopic sleeve gastrectomy may contribute to improved decision-making after surgery. Interestingly, after surgery, increased insula activation correlated with reduced scores on the disinhibition subscale of the Three-Factor Eating Questionnaire (TFEQ; Stunkard & Messick, 1985), where higher scores indicate a greater loss of control over food intake (Zhang et al., 2023). The insula is a central neural substrate of interoception (Craig, 2002, 2009) modulating decision-making by integrating interoceptive information (Volkow & Baler, 2015). Enhanced insula activation may indicate a compensatory effect, suggesting that increased interoception in obese individuals reduces impulsive food choices (i.e. delay discounting). However, this effect of interoception on delay discounting specifically emerged post-surgery. Nevertheless, these findings lay a foundation for further research into how bolstering interoception can mitigate maladaptive decisions resulting from delay discounting using nonoperative treatments (Zhang et al., 2023). Insula activation has emerged as a protective factor also in addiction, notably alcohol use disorder (Halcomb et al., 2022). Analogous to observations in obesity (Amlung et al., 2016), individuals grappling with addiction exhibit a propensity for immediate rewards while devaluing future outcomes, resulting in steeper delay discounting (Bickel & Marsch, 2001). Positioned as a key node of the salience network, particularly the anterior insula is responsible for mediating interoceptive and attentional shifts toward salient stimuli and their valuation (Halcomb et al., 2019). Moreover, the salience network is implicated in delay discounting (Frost & McNaughton, 2017), and alterations within this network are noted in individuals with alcohol

use disorder, directing increased attention towards interoceptive cues of intoxication (Halcomb et al., 2019). Building up on these insights, Halcomb and colleagues (2022) tested anterior insula activation in heavy drinkers and its correlation with delay discounting behaviors and alcohol consumption patterns. Mirroring findings in the realm obesity (Zhang et al., 2023), heightened activation in the insula (anterior) during intertemporal choices is associated with a reduction in impulsive decision-making concerning alcohol intake (Halcomb et al., 2022).

5.3.3 Emotions as mediators of Interoception's impact on Delay Discounting

Research suggests that impulsive or addictive behaviors, such as binge eating, heavy drinking, or smoking, often serve as maladaptive attempts to alleviate negative affective mood states (Abrantes et al., 2008; M. L. Cooper et al., 1995; Smyth et al., 2007). Moreover, it is widely acknowledged that visceral bodily sensations contribute significantly to affect and emotional experiences (Garfinkel & Critchley, 2013). In the realm of intertemporal choices, the desirability (i.e. subjective value) of different options is influenced by affective visceral mechanisms, underscoring the role of emotions as a crucial interface between delay discounting and interoception (Loewenstein, 1996). Scarpazza and colleagues (2017) explored this relationship within the context of **alexithymia**, a personality trait that emerges at variable degree in the general population (Kokkonen et al., 2001) and is characterized by impaired emotional understanding and regulation (van der Velde et al., 2015). Frequently co-occurring with clinical conditions marked by poor interoception such as eating disorders (e.g. Carano et al., 2006) and substance abuse (e.g. Mann et al., 1995), alexithymia has been associated with a general failure in interoception (Brewer et al., 2016). In their study Scarpazza and colleagues (2017) adopted the heartbeat perception task (Schandry, 1981) to measure interoceptive sensibility, alongside a monetary delay discounting task, in individuals with varying degrees of alexithymia. They found that individuals with higher levels of alexithymia displayed steeper delay discounting

compared to those with lower levels of alexithymia. Surprisingly, contrary to earlier assumptions (Brewer et al., 2016), individuals with high levels of alexithymia exhibited greater interoceptive sensibility (Scarpazza et al., 2017). This could be explained by the somatosensory amplification model of alexithymia positing that individuals experience amplified bodily sensations (e.g. heart rate) without fully integrating them into higher levels of emotional processing (Nakao et al., 2002; Scarpazza et al., 2017). Furthermore, greater interoceptive sensibility was correlated with increased discount rates, suggesting that the heightened representation of internal bodily signals in high alexithymia individuals (heartbeat) results in a more impatient behavior (Scarpazza et al., 2017). In the context of alexithymia, one might expect that overall deficits in interoception would correlate with higher rates of discounting, as commonly seen in clinical conditions (Brewer et al., 2016). However, the aforementioned findings suggest otherwise, indicating that higher discount rates are actually associated with heightened, rather than impoverished interoceptive sensibility (Scarpazza et al., 2017). How can these inconsistencies be reconciled? During decisions involving time trade-offs, individuals anticipate the emotions linked to each choice option, producing bodily and visceral changes. Therefore, rather than a general interoceptive deficit, difficulties accurately predicting these future internal states may contribute to the devaluation of delayed rewards. Consequently, individuals with elevated levels of alexithymia may be biased to immediate rewards due to experiencing amplified bodily sensations, coupled with an inability to predict forthcoming interoceptive experiences (Scarpazza et al., 2017; Sellitto et al., 2016; Starita et al., 2016). Nevertheless, other research delving into the influence of emotions on the interplay between delay discounting and interoception has shown that heightened interoceptive sensibility correlates with lower rates of discounting. This increased awareness of bodily sensations in turn is linked to emotional arousal. Thus, during moments in which individuals are more aware of their bodily sensations that trigger affective responses, they tend to discount future rewards less (Kochanowska et al., 2023). Additionally,

negative emotions or emotional distress are associated with increased interoceptive sensibility, often leading individuals to seek immediate pleasure (Herman et al., 2018a), whereas positive mood states are related to less impulsive choices, making individuals more patient (Weafer et al., 2013). While the role of emotions in intertemporal decision-making remains somewhat ambiguous, it is evident that affective states stemming from interoceptive processes can influence impulsive behavior and thus delay discounting. A comprehensive understanding of their regulatory role is crucial for devising effective coping strategies for impulsive individuals to facilitate more favorable decision-making in everyday life (Herman et al., 2018a, 2018b; Kochanowska et al., 2023).

Interoception deficits are implicated in clinical conditions characterized by poor decision-making, marked by a repeated preference for immediate gratification over long-term health benefits (Herman et al., 2018a; Khalsa et al., 2018; Tsakiris & Critchley, 2016). While neuroimaging studies highlight the critical role of the insula in time-sensitive decisions (Fu et al., 2022; Naqvi et al., 2007; Sellitto et al., 2016), some behavioral evidence emphasizes the significance of emotions (Kochanowska et al., 2023; Scarpazza et al., 2017; Weafer et al., 2013). Both the insula and emotions are implicated not only in intertemporal choices but also related to individuals' awareness of their internal bodily sensations, underscoring the link between interoception and delay discounting (Craig, 2002, 2009; Scarpazza et al., 2017; Sellitto et al., 2016). While inconsistencies persist regarding the precise nature of these links, these findings hold significance for clinical practice, highlighting the need for further research. Specifically, interventions targeting the insula may mitigate maladaptive aspects of intertemporal decision-making commonly observed in conditions such as addiction (Halcomb et al., 2022; Sellitto et al., 2016; Zhang et al., 2023). Knowing when to rely on one's "gut feelings" or when to "listen to the heart" can profoundly impact people's decision-making behavior (Dunn et al.,

2010; Werner et al., 2009), particularly in situations involving a choice between immediate gratification and long-term health outcomes.

6 The relationship between Memory and Delay Discounting

The preceding chapter highlighted the importance of emotional states in impulsive decision-making, proposing that negative emotions correlate positively with bodily awareness (i.e. interoception) and predispose individuals toward short-sighted choices, which can ultimately result in adverse health outcomes such as obesity and substance abuse. Additionally, it is conceivable that individuals experiencing negative emotions may exhibit a memory bias, causing them to recall past instances of impulsive behavior, thus priming them to repeat similar actions (Herman et al., 2018a). Furthermore, emotions play a crucial role, particularly in autobiographical memory, as they modulate the reliving of encoded events (R. A. Cooper et al., 2019; Tulving, 2005). **Autobiographical memory** pertains to the recollection of events that constitute an individual's personal experiences (Svoboda et al., 2006), and emerging evidence suggests that interoception contributes to the formation of these memory engrams associated with the self by facilitating feelings of re-experiencing an event (Allman & Mareschal, 2016; Messina et al., 2022). Moreover, autobiographical events are recalled as more emotionally intense and positive autobiographical memory retrieval has been found to increase positive affect (Messina et al., 2022; Speer et al., 2014). However, emotions influence memory processes not only in remembering the past but also in perspective thinking, as imagining negative future events leads to increased delay discounting (Liu et al., 2013). Thus, emotions contribute to both interoception (e.g. Kochanowska et al., 2023) and memory (e.g. R. A. Cooper et al., 2019), with interoception also affecting delay discounting – as highlighted in chapter 5 – and memory (Messina et al., 2022). Given these connections, it is now pertinent to investigate whether memory itself plays a critical role in promoting more patient choices (Lempert et al., 2017). Therefore, the following sections of this chapter will explore two possible cognitive manipulations that may reduce delay discounting: **imagining the future and remembering the positive past.**

6.1 Imagining the future: Leveraging Episodic Future Thinking to reduce impulsive choices

How do memory processes involved in imagining the future impact delay discounting? According to Tulving's research (1985), episodic memory, which is often the focus of studies on humans' ability to recall past experiences (Tulving, 2002) provides the foundation for mentally traveling in time to both the past and the future (Tulving, 1985). Since our world is dynamic, predicting future events can offer a selective advantage for survival (Suddendorf & Corballis, 2007) and, as previously described, neglecting the future when making decisions can negatively impact individuals' health (Frederick et al., 2002). The capacity to vividly imagine or simulate one's own future is termed **episodic future thinking** (Ciaramelli et al., 2019; Rung et al., 2018; Schacter et al., 2017; Szpunar, 2010), also referred to as **mental time travel** or **perspective thinking** (Bar, 2009; Szpunar, 2010). The crucial function of episodic memory in simulating or imagining future events is to provide the necessary information to build alternative perspectives and conceive future situations. This ability to shift one's perspective from the immediate present to alternative viewpoints is called self-projection, an important component in episodic future thinking (Buckner & Carroll, 2007; Schacter et al., 2007). Several studies suggest that the capacity for episodic future thinking may underlie humans' ability to make farsighted choices, favoring long-term benefits and thus reducing delay discounting (e.g. Boyer, 2008; Peters & Büchel, 2010a). In a study by Peters & Büchel (2010a), participants performed a classic delay discounting task (control condition) alongside a novel (episodic) condition that involved the presentation of cue words referring to subject-specific future events for the respective delay of rewards (e.g. "birthday John"), obtained during a pre-scan interview. When participants were cued to pre-experience future events, they discounted future rewards significantly less compared to the control condition (i.e. episodic tag effect; Peters & Büchel, 2010a).

At the neural level, a substantial body of research suggests a core brain system crucial for mediating episodic future thinking. This network encompasses medial prefrontal regions, medial and lateral parietal cortex, the PCC, retrosplenial cortex, lateral temporal cortex, and the medial temporal lobe (Schacter et al., 2007; Szpunar et al., 2007). Notably, regions within this core network are functionally linked with the hippocampal formation (Schacter et al., 2007), which plays an important role in forming vivid event representations (Schacter & Addis, 2009) and enabling self-projection into the future by facilitating the evaluation of future payoffs through mental simulation (A. Johnson et al., 2007). The hippocampus is integral to both episodic future thinking and decision-making (A. Johnson et al., 2007), with studies showing that hippocampal damage can result in disadvantageous decision-making (Gupta et al., 2009). Interestingly, another medial temporal lobe region – the amygdala – has been implicated in impaired decision-making, with lesions often resulting in maladaptive choices (Winstanley et al., 2004). Peters and Büchel's (2010a) study further supports the importance of these regions in intertemporal decision-making and episodic future thinking. Alongside the behavioral analyses, the authors also investigated the neural mechanisms that mediate the effect of episodic future thinking on delay discounting. Their findings demonstrated that the episodic tag effect correlated with subject-specific imagery scores, indicating that the effect was more pronounced with vivid visualization. Furthermore, fMRI data yielded that brain activity in the ACC and neural coupling between ACC and the hippocampus and amygdala predicted the magnitude of the episodic tag effect, influencing how much individuals shifted their preferences towards the future (Peters & Büchel, 2010a). Both the hippocampus and amygdala are extensively interconnected with the VS and vmPFC (Haber & Knutson, 2010), which form the valuation network outlined by Peters and Büchel (2011). As described earlier, Peters and Büchel (2011) emphasized that distinct neural networks contribute to intertemporal decision-making: a valuation network and a cognitive control network (i.e. lateral PFC and ACC). Based on previous evidence

which implicated hippocampus and amygdala being involved in delay discounting as well, they proposed a third important network contributing to intertemporal choices, the medial temporal lobe network. This network is believed to play a role in delay discounting by representing potential future outcomes of decisions. Thus, their model predicts that episodic future thinking, valuation, cognitive control and medial temporal lobe networks, reduce impulsivity in intertemporal choices (Peters & Büchel, 2011). These insights prompt further exploration of how episodic future thinking can be leveraged to help highly impulsive individuals with high discount rates, such as those with obesity or addictions.

6.1.1 Episodic Future Thinking in addressing obesity and addiction

The first evidence that episodic future thinking can reduce delay discounting in **overweight and individuals with obesity** was provided by Daniel and colleagues (2013). Similar to Peters and Büchel (2010a), participants in the episodic future thinking condition were asked to envision potential future events corresponding to the delays in the delay discounting task. Control participants engaged in an imagery task based on events described in a travel blog (Daniel et al., 2013b). Additionally, the study included an ad libitum eating task, simulating a tempting food-related scenario with unlimited food access potentially triggering impulsive consumption for immediate gratification. Results showed that participants in the episodic future thinking condition discounted future rewards less and consumed fewer calories during the ad libitum task compared to those in the control condition. Furthermore, despite neurophysiological differences between obese and lean individuals, such as decreased cerebral blood flow in regions associated with episodic future thinking in obese individuals (Willeumier et al., 2011), which could potentially blunt the effect of episodic future thinking, there was no significant difference in its effectiveness between these two groups (Daniel et al., 2013a). Therefore, episodic future thinking proves to be a powerful tool for reducing both delay discounting and

energy intake in obese individuals, suggesting its potential as a self-regulatory skill for maintaining a healthy body weight and for obesity treatment (Daniel et al., 2013b, 2013a).

Episodic future thinking also serves as a powerful aid in addressing **addiction**. Individuals with alcohol dependence exhibit steeper discount rates compared to controls (Petry, 2001a) and may also experience deficits in future thought, as prospective memory negatively correlates with the magnitude of dependence (Griffiths et al., 2012). Imagining future events has been shown to improve prospective memory (Griffiths et al., 2012), prompting Snider and colleagues (2016) to examine the effects of episodic future thinking on delay discounting and alcohol purchase behavior in individuals with alcohol dependence. In their study, participants either generated positive future events (episodic future thinking condition) or recent past events (control condition), which were used as cues during a delay discounting task. Both groups also engaged in an alcohol purchase task, imagining themselves in a bar scenario and indicating how many hypothetical drinks they would buy (Snider et al., 2016). Consistent with findings regarding obesity (Daniel et al., 2013b, 2013a), the results revealed that episodic future thinking reduces delay discounting and hypothetical alcohol consumption when drinks were free or at very low cost, indicating a lower demand intensity (Snider et al., 2016).

Together, this evidence suggests that episodic future thinking may widen individuals' temporal perspectives, leading them to value future outcomes more and make **more self-controlled decisions** (Daniel et al., 2013b, 2013a; Peters & Büchel, 2010a; Snider et al., 2016). However, as the effectiveness of episodic future thinking on reducing delay discounting is linked to the vividness of the imagined events (Peters & Büchel, 2010a), Daniel and colleagues (2013a) posited that imagining the future may require personal salience. Personal salience is a crucial aspect of autobiographical memory, characterized by the recollection of events from one's own history, which are of greater personal significance (Svoboda et al., 2006). In line

with this, Ciaramelli and colleagues (2019) found that mental time travel is more effective in subjects that could imagine future events more vividly. Therefore, the crucial role of vividness and personal salience indicates that autobiographical memory may be another tool to modulate delay discounting.

6.2 Remembering the positive past: The role of Autobiographical Memory retrieval in promoting patient choices

Individuals tend to make more patient choices when they imagine positive future events during or prior to intertemporal decision-making (Daniel et al., 2013b, 2013a; Peters & Büchel, 2010a; Snider et al., 2016). Interestingly, there is an overlap in the neural bases implicated in episodic future thinking and remembering the past, with autobiographical memory retrieval relying on the same circuitry (i.e. mPFC, PCC, medial temporal lobe etc.), indicating that autobiographical memory could be a promising target for reducing delay discounting (Lempert et al., 2017; Spreng et al., 2009). Indeed, along with several other cognitive processes, successful decision-making requires drawing on personal experiences, enabling individuals to recall similar past situations and the consequences associated with these decisions (El Haj et al., 2020). To test the potential influence of autobiographical memory on delay discounting, Lempert and colleagues (2017) investigated whether recalling autobiographical memories can promote patient choices. Participants were instructed to recall positive autobiographical memories prompted by different life events such as ‘family vacation’, summarized in subject-specific event cues. These cues were then used in a delay discounting task, which included memory and control blocks. In the memory condition, participants were presented with the cues and asked to recall and elaborate on the corresponding memory before making an intertemporal choice. In control blocks, participants rated their tiredness, boredom and feelings. Results revealed that autobiographical memory retrieval reduces delay discounting, with the effect being specific to

positive, not negative, memories (Lempert et al., 2017). Although research on the effects of positive autobiographical memory retrieval on delay discounting is relatively scarce, El Haj and colleagues (2020) explored the relationship between delay discounting and disease-related decline in autobiographical memory in patients with Alzheimer's Disease (AD), a population characterized by high discount rates (Thoma et al., 2017). Consistent with previous evidence (Thoma et al., 2017), AD patients showed greater delay discounting compared to control older adults. Furthermore, the study found a significant negative correlation between delay discounting and autobiographical memory in patients with AD, indicating that their difficulties in remembering information about past decisions led them to opt for immediate gratification (El Haj et al., 2020).

6.3 Neither the past nor the future: Detachment from the present may alter Delay Discounting

While studies have shown that recalling the positive past and imagining positive future events can reduce delay discounting, Ciaramelli and colleagues (2019) provided new insights, suggesting that neither the future nor the past is determining this effect. As previously mentioned, self-projection is an important processing component in mental time travel (Lempert et al., 2017; Schacter et al., 2007). Yet, engaging in self-projection requires the detachment from one's direct perceptual experience, indicating that this process itself may be responsible for altering delay discounting (Ciaramelli et al., 2019). In their study, Ciaramelli and colleagues (2019) asked participants to imagine future events, recalling past events, imagine an alternative present event, or focus and report on their current experience. They then made intertemporal choices regarding food and money. Interestingly, all time conditions (i.e. future, past, and present) were equally associated with a decrease in delay discounting compared to focusing on the current experience. Furthermore, this effect was only observed in individuals who were able to

vividly imagine the mentally constructed events. According to the authors, shifting individuals' perspective by self-projecting into a constructed experience can help resist the temptation of immediate gratification and favor future outcomes (Ciaramelli et al., 2019).

Humans face intertemporal choices daily and often prioritize immediate gratification over future benefits, leading to delay discounting (e.g. Daniel et al., 2013b). This tendency to devalue future consequences can lead to maladaptive behaviors and negative health outcomes, such as obesity and addiction, highlighting the need to find strategies to reduce delay discounting (Frederick et al., 2002; Lempert et al., 2017). Two promising approaches are recalling positive autobiographical memories (Lempert et al., 2017) and engaging in episodic future thinking (Peters & Büchel, 2010a). Both techniques have been found to reduce delay discounting, making them potential targets for developing interventions and treatments aimed at mitigating adverse health outcomes (Daniel et al., 2013b, 2013a; El Haj et al., 2020; Lempert et al., 2017). However, it may be the mental construction of vivid events themselves that reduces delay discounting. Irrespective of their temporal location (past, future, or present) these imagined events, which differ from ones' current perceptual experience, can diminish the tendency to indulge in immediate gratification. This indicates that self-projection could be a potential protective factor against impulsive decision-making (Ciaramelli et al., 2019).

7 Discussion

Intertemporal choices – decisions involving a tradeoff between costs and benefits distributed over time – are a fundamental component of people’s everyday life, shaping their daily routines and impacting their future. Within this context, humans typically tend to prefer smaller, immediate over larger, later rewards (i.e. delay discounting) (Sellitto et al., 2011). Indulging in immediate gratification while devaluing future rewards is related to impulsivity, characterized by an inability to wait for delayed rewards (Takahashi et al., 2007). Individuals with higher delay discounting often show greater impulsivity and impaired self-control (Takahashi et al., 2007), both of which are related to pathological conditions such as obesity (Schiff et al., 2016) and addiction (e.g. Bickel et al., 1999; Kirby & Petry, 2004). These maladaptive behaviors underscore the need for strategies to reduce delay discounting and for promoting future-oriented decision-making in these individuals.

7.1 Discrepancies in research on the effects of Interoception and Memory on Delay Discounting

This thesis focused on both the connection between delay discounting and interoception, as well as the relationship between delay discounting and memory-related processes such as episodic future thinking or autobiographical memory collection, as promising targets to alter the degree of delay discounting. Evidence regarding interoception remains somewhat inconsistent. While lesion studies indicate that insula damage results in decreased delay discounting (e.g. Sellitto et al., 2016), neuroimaging studies revealed that increased insula activation, and therefore supposedly enhanced interoception, leads to decreased delay discounting (Halcomb et al., 2022; Zhang et al., 2023). Similar discrepancies emerge in behavioral studies focusing on emotions, showing that increased interoceptive sensibility is associated with steeper delay discounting in alexithymic individuals (Scarpazza et al., 2017), yet it also correlates with lower

discount rates (e.g. Kochanowska et al., 2023). Despite evidence for memory-related changes in delay discounting, there are some inconsistencies also in this area of research. For example, Ciaramelli and colleagues (2019) found that delay discounting is reduced when individuals mentally construct vivid events that differ from their immediate perceptual present, regardless of the events' temporal location. Additionally, Lempert and colleagues (2017) discovered that recalling positive autobiographical memories before making intertemporal choices leads to more future-oriented decisions. However, they could not replicate these findings in subsequent studies, raising questions on the robustness and generalizability of the effects of autobiographical memory retrieval on delay discounting (Lempert et al., 2024). Due to the non-significant and small effects on delay discounting, the authors therefore suggest to use autobiographical memory retrieval as control condition in studies investigating the effect of episodic future thinking rather than as an experimental manipulation itself (Lempert et al., 2024). Discrepancies also emerge regarding the effect of episodic future thinking on delay discounting, especially in the realm of addictions. Snider and colleagues (2016) found that episodic future thinking reduced impulsive choices in individuals with alcohol dependence. Contrary, Rung and Madden (2018) indicated that episodic future thinking may not be effective for this population, given that substance-dependent individuals usually have lower working memory capacity (e.g. Bechara & Martin, 2004), which negatively impacts the effectiveness of episodic future thinking (Lin & Epstein, 2014). Considering the evidence on the relationship between interoception and delay discounting, as well as the connection between memory and delay discounting, and the discrepancies that have emerged in these areas, some important questions arise: Are there intersections between these three domains? And can combining the insights gained from interoception and memory research provide a promising approach for developing interventions to reduce delay discounting?

7.2 Potential intersections between Delay Discounting, Interoception, and Memory

In the context of interoception, the **interoceptive predictive coding model** (Seth et al., 2012) provides a different perspective on emotions, positing that emotional states result from predictions about future interoceptive states of one's own body. According to the model, the anterior insula, a region implicated in interoceptive awareness, is a core neural correlate in interoceptive prediction. Interestingly, the anterior insula is structurally and functionally interconnected with brain regions involved in reward-related decision-making, such as the ACC and the OFC (Seth et al., 2012). This indicates that the model could provide further explanations for the relationship between interoception and delay discounting. Scarpazza and colleagues (2017) hypothesized that the devaluation of future rewards in individuals with alexithymia might be caused by their inability to predict interoceptive states. Similarly, Sellitto and colleagues (2016) argue that by predicting the emotional and bodily effects of different alternatives, the insula may signal the urge for immediate gratification. The ability to anticipate one's future affective states is essential for accurately valuing a future reward (Scarpazza et al., 2017), as the anticipation of emotional or bodily effects from receiving a future reward influences its subjective value (Sellitto et al., 2016). According to Seth and colleagues (2012), the interoceptive predictive coding model may be one key feature of an integrated self-representation and sense of selfhood. Self-representation is thought to arise from the interaction of two neural systems: the mirror neuron system and the **default mode network (DMN)** (Molnar-Szakacs & Arzy, 2009). The DMN is engaged during passive tasks without directed goals, specifically when individuals shift from focusing on the external environment to an undisturbed internal mode of thinking (Buckner et al., 2008; Buckner & Carroll, 2007). Notably, the DMN encompasses several brain regions that are also part of the core brain network for episodic future thinking such as prefrontal regions, medial and lateral parietal regions, the PCC, retrosplenial cortex, and the medial temporal lobe (Buckner & Carroll, 2007; Spreng et al., 2009). The same

network is activated when remembering the past (Spreng et al., 2009) aligning with evidence showing that patients with amnesia are impaired in both recalling past events and imagining the future, particularly regarding self-related events or information (Hassabis et al., 2007; Klein et al., 2002). Remembering the past and imagining the future are cognitive abilities related to **self-projection**. Self-projection involves not only shifting perspectives from now to then, but also refers to transposing “the effective reference point from self to other [and] from here to there” (Mesulam, 2002, p. 22), thus also contributing to imagining the viewpoint of others (i.e. theory of mind) and spatial navigation, which involves simulating another perspective or a mental map of the environment (Buckner & Carroll, 2007). This supports evidence suggesting that shifting perspectives by self-projecting into a mentally constructed experience different from the immediate present can lead to more farsighted choices by reducing delay discounting, irrespective of the temporal location (Ciaramelli et al., 2019). However, the time domain remains crucial, as mentally constructing alternative perspectives is based on one’s past experiences, thus relying on autobiographical memory (Buckner & Carroll, 2007). Interestingly, a study on hippocampal-lesioned patients, who are typically impaired in both backward and forward mental time travel, found that these patients did not show different discounting behavior compared to control participants (Kwan et al., 2012). This suggests that the ability to imagine future rewards is not the only process sustaining discounting behavior (McCormick et al., 2018). The overlapping brain regions activated by all these processes are part of the DMN, highlighting its adaptive role in representing self-projection by using individuals’ past experiences to plan for the future (Buckner & Carroll, 2007). Since the DMN is also implicated in self-representation associated with the interoceptive predictive coding model (Molnar-Szakacs & Arzy, 2009; Seth et al., 2012), it might play a role in interoception and therefore represent an important intersection between delay discounting, memory, and interoception. Evidence implicating the DMN in interoception comes from studies with patients with anorexia nervosa (AN), who are

characterized by increased interoceptive awareness (Kaye et al., 2009) and lower discount rates compared to healthy controls (Steinglass et al., 2017). Notably, Boehm and colleagues (2014) found increased functional connectivity between the DMN and the anterior insula in AN, which in turn has been found to be hyperactivated in AN (Kaye et al., 2009). As observed in AN (e.g. Kaye et al., 2009), insula activation and interoceptive awareness go hand in hand with decreased delay discounting in obesity (Zhang et al., 2023) and addiction (Halcomb et al., 2022). Thus – considering the beforementioned evidence regarding the interconnection of the insula with the DMN – both the insula and the DMN may be key targets for interventions aiming at altering delay discounting.

7.3 Combining insights from Interoception and Memory research to inform Delay Discounting intervention strategies

Mindfulness-based interventions involving instructions in practices such as focusing on breathing, one’s heartbeat, or sensory experiences (Datko et al., 2022; Haase et al., 2016), have been shown to increase insula response and interoceptive awareness (Datko et al., 2022; Lima-Araujo et al., 2022; Sharp et al., 2018). Applying this to **obesity**, typically characterized by an interoceptive deficit leading to reduced sensitivity to satiety signals and maladaptive food-related decisions (Martin et al., 2019), mindfulness-based interventions provide a promising tool to address this issue and have already been successful in weight loss interventions (Katterman et al., 2014). Similarly, mindfulness-based interventions have been successfully used for the treatment of **addiction**, reducing substance use and craving (Witkiewitz et al., 2013). Enhancing interoceptive abilities through mindfulness may also contribute to autobiographical memory retrieval, as Messina and colleagues (2022) found that individuals with high interoceptive sensibility recalled autobiographical events more specifically and vividly. This is significant because the DMN relies on one’s past experiences (i.e. autobiographical memories)

when constructing alternative perspectives such as imagining future events (Buckner & Carroll, 2007), which has been shown to reduce delay discounting in both individuals with addictions (Snider et al., 2016) and obesity (Daniel et al., 2013b, 2013a). To date, no studies have investigated the potential interconnections between memory, interoception, and delay discounting. Yet, combining mindfulness training and episodic future thinking could provide valuable insights for developing intervention strategies to reduce delay discounting. Individuals could undergo a mindfulness training to enhance their interoceptive awareness, which would help focusing on bodily signals associated with imagining a positive future event. This procedure would potentially recruit a broad network, including the insula and the DMN, which may help individuals anticipating future rewards in a more appropriate way and increasing their willingness to delay gratification. However, for individuals with addictions, incorporating an additional working memory training may be useful to address the potentially blunted effect of episodic future thinking due to their impaired working memory (Lin & Epstein, 2014). In conclusion, enhancing individuals' interoceptive awareness through mindfulness training combined with adopting episodic future thinking in future studies could provide valuable insights for developing interventions targeting clinical populations characterized by high discount rates such as individuals with obesity and addiction. Individuals undergoing the proposed procedure could effectively process their bodily sensations, recognizing feelings of craving without succumbing to the temptation and thereby prioritizing future health benefits (see **Figure 8** for a schematic summary).

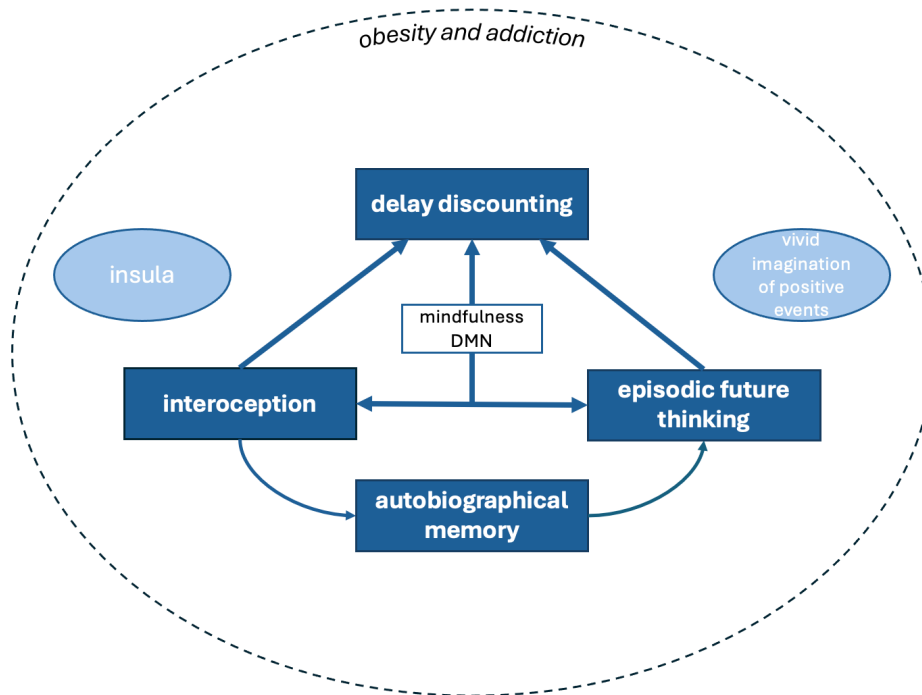


Figure 8. Schematic representation of delay discounting and its relationship with interoception and memory. The insula plays a crucial role in altering delay discounting, as increased activation is related to enhanced interoception and decreased delay discounting. Episodic future thinking, particularly the vivid imagination of positive future events, has also been shown to reduce delay discounting. High interoceptive sensibility enables a more specific and vivid recollection of autobiographical memory, which forms the basis for constructing alternative perspectives such as imagining future events. Combining interoception and memory manipulations within an intervention, including mindfulness training and the activation of the DMN through episodic future thinking, could potentially reduce delay discounting for example in clinical populations, such as individuals with obesity or addiction.

7.4 Limitations and future directions

This thesis focused on the relationship between delay discounting, interoception, and memory-related processes, primarily in the context of obesity and addictions. However, delay discounting is a trans-disease process related to a wide range of disorders beyond obesity and addictions (Koffarnus et al., 2013). For example, high discount rates are also observed in psychiatric and developmental disorders such as attention deficit hyperactivity disorder (e.g. Wilson et al., 2011), anxiety (Rounds et al., 2007), and schizophrenia (e.g. MacKillop & Tidey, 2011). Investigating the influence of interoception and memory-related processes on delay discounting in these conditions should therefore be a goal for future research.

Another limitation of this thesis is the focus on adult participants. There are considerable differences in the degree of delay discounting across lifespan. While adolescence is marked as a highly impulsive period (Arnett, 1999), delay discounting tends to decrease in older adulthood (Green, Fry, et al., 1994). Additionally, the ability to delay gratification in preschool age predicts later life outcomes such as academic performance and stress management (Mischel et al., 1988). Future studies should further investigate the developmental course of delay discounting, as well as of episodic future thinking abilities and interoceptive awareness across lifespan, and possibly determine if manipulations like episodic future thinking or combined approaches with interoception are effective in highly impulsive age subgroups such as adolescents.

8 Conclusion

This thesis addressed the relationship between delay discounting, interoception, and memory. Devaluing future rewards in favor of immediate gratification can lead to maladaptive behaviors in both healthy and clinical populations characterized by impulsive decision-making, such as individuals with obesity or addiction. As a trans-disease process, delay discounting is crucial to various clinical conditions beyond obesity and addiction. Therefore, it is important to address it by interventions that enhance interoceptive abilities, or by memory-related procedures like episodic future thinking, both of which have been shown to reduce delay discounting. Although much remains to be researched, combining interoceptive approaches with episodic future thinking may provide a promising strategy for improving maladaptive decision-making patterns and therefore promoting a healthier lifestyle in both clinical and non-clinical populations.

Disclosure Note:

ChatGPT was used for language purposes only, specifically for generating synonyms and checking grammar in a few single sentences.

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